Life history differences in age-dependent expression of multiple ornaments and behaviors in a lekking bird

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Abstract

Age is a major factor explaining variation in life history traits among individuals with typical patterns of early life improvement, prime age and senescence in reproductive success and survival. However, age-dependent variation in the expression of sexually-selected traits has received less attention although such variation underpins differences in male competitive abilities and female preference that are central to sexual selection. Contrary to previous studies focusing on single traits, we used repeated measures of seven sexually-selected morphological and behavioral traits in male black grouse (*Tetrao tetrix*) to quantify the effects of age and lifespan on their expression, and quantified this variation in relation to male reproductive effort. Trait expression increased with age but long-lived males had slower increase and delayed maxima in trait values compared to short-lived males. There was evidence of terminal investment (increasing trait value during the last breeding season) in some and senescence in all traits. These trait dynamics were largely explained by the timing of male peak lekking effort. This study shows that fully understanding the variation in sexually-selected traits and fitness benefits associated with sexual selection requires accounting for the complex interaction between individual age, lifespan and the timing of individuals' investment in reproduction.

Introduction

Age-dependent variation in life history traits, secondary sexual traits and behavior is widespread, with typical patterns of early life improvement, prime age maximum expression and senescence (Manning 1985; Andersson 1994; Brooks and Kemp 2001; Jones et al. 2008; Nussey et al. 2013). The variation in the duration of each stage and/or the shape of individual trajectories often depend on species' life history and might result from differences in individuals' allocation strategies. Despite the increasing understanding of the age-dependent variation in trait expression, little is known about mechanisms underlying such variation and their implications for sexual selection (Bonduriansky et al. 2008; Monaghan et al. 2008; Nussey et al. 2013).

Until recently, longitudinal studies of age-dependent variation in individual performance and trait expression have been scarce as long-term data with repeated measures of individuals are extremely laborious to collect (Clutton-Brock and Sheldon 2010). However, only longitudinal studies can separate within-individual (i.e. phenotypic plasticity, individual improvement, senescence) and between-individual effects (i.e. selective appearance or disappearance of certain phenotypes) of age on trait expression (van de Pol and Verhulst 2006; van de Pol and Wright 2009). As individual trajectories can be hidden by demographic heterogeneity (Bouwhuis et al. 2009; van de Pol and Wright 2009; Evans et al. 2011), neglecting within-individual effects might lead to incorrect conclusions about the effects of ageing on life histories.

The application of mixed models on longitudinal data has bypassed this major limitation and revealed that within- and between-individual effects can differ in many situations, and that both can result in a positive association between age and trait expression at the population level (van de Pol and Verhulst 2006; van de Pol and Wright 2009; Rebke et al. 2010). Most of the recent longitudinal studies focused on key life

history traits, such as reproductive success (e.g. Dugdale et al. 2011; Froy et al. 2013), and survival (e.g. Bouwhuis et al. 2012), but there is growing interest in age-dependent variation in secondary sexual traits (Balbontín et al. 2011; Evans et al. 2011) and behavior (Mainguy and Côté 2008; Nussey et al. 2009). This is crucial, because secondary sexual traits act as honest indicators of individuals' overall genetic quality if their elaboration and maintenance are associated with fitness costs, which in turn depend on individual body condition (Zahavi 1975; Kotiaho 2001). Moreover, life history theory predicts that when resources are limited, all fitness components cannot be maximized simultaneously due to trade-offs. Individuals are consequently expected to adjust their trait expression according to their condition, and excess allocation on sexual traits or behavior can trade off with survival or reproductive success. (Stearns 1992; Reznick et al. 2000). Hence, only longitudinal studies can reliably quantify the degree to which variation in the expression of these traits with age can explain a large proportion of the variation in individual fitness.

Although longitudinal studies on age-dependent variation in trait expression are accumulating across a wide range of taxa (e.g. Coltman et al. 2002; Hoikkala et al. 2008; Nussey et al. 2009; Massot et al. 2011; Vande Velde 2011), mechanisms behind these patterns are often not thoroughly understood (Monaghan et al. 2008; Nussey et al. 2013). In particular, previous studies have focused on socially monogamous birds with limited potential for sexual selection (e.g. Balbontín et al. 2011; Evans et al. 2011; Bouwhuis et al. 2012; Froy et al. 2013). However, since male-male competition and female choice can dampen or strengthen the effects of ageing on life histories (Bonduriansky et al. 2008), patterns of age-dependent trait expression in these species with low variation in male mating success may differ substantially from those observed in species with strong sexual selection. Moreover, many previous studies have focused on single sexually-selected traits (e.g. antler size, Nussey et al. 2009; tail feather length, Balbontín et al. 2011). However, sexual selection is clearly a multifaceted process, so investigating multiple traits

simultaneously is needed to unravel the constraints and trade-offs acting on these traits (Evans et al. 2011) and to accurately quantify the overall fitness costs of trait expression (Kotiaho 2001; Lecomte et al. 2010). Finally, age-dependent expression of sexual traits has not yet been quantified in relation to temporal scheduling of individual reproductive effort, where peak reproductive effort is expected to differ among individuals depending on their current body condition and hence may be the only opportunity during which all traits are expressed at their maximum. Therefore, longitudinal studies on species with multiple sexual traits quantifying age-dependent expression of these traits in relation to the timing of reproductive effort are needed to fully understand the effects of age on individual trait expression and their consequence for sexual selection.

The black grouse (*Tetrao tetrix*) is a relatively short-living lekking galliform (< 2 % of recruited individuals live 5 years or longer) with intense male-male competition, and female choice is a major factor driving the evolution of the expression of multiple male sexual traits (Alatalo et al. 1991, 1992). In particular, females prefer mating with males that are most present on the leks (Alatalo et al. 1992), fight frequently and successfully against other males (Hämäläinen et al. 2012) and occupy central territories (Hovi et al. 1994). Males with the greatest body mass loss during the lek have highest fighting rate (Hämäläinen et al. 2012), mating success and most central territories (Lebigre et al. 2013) indicating that strong physiological costs of male display mediate the honesty of these traits. Furthermore, lyre (i.e. tail) length and quality (Höglund et al. 1994), the size of the testosterone induced red eye combs (Alatalo et al. 1996) and blue chroma coloration of breast feathers (Siitari et al. 2007) are all positively correlated with male mating success. The distribution of male annual mating success is highly skewed, with few dominant males monopolizing nearly all copulations, whereas the majority of males, especially yearlings do not mate (Alatalo et al. 1992; Kervinen et al. 2012). Consequently, male lifetime mating success is similarly skewed, and most males fail to contribute genetically to the next

generation. Therefore, the lekking black grouse is an outstanding natural system to study the age-dependent expression of multiple morphological traits and behaviors in relation to sexual selection.

We first tested the hypotheses that male trait expression depends both on male age and lifespan, and expected that males with high early life trait expression had shorter lifespans. We therefore quantified the age-dependent expression of multiple morphological and behavioral traits and separated the effects of within-individual improvement and senescence from selective appearance and disappearance of certain phenotypes in the population. To compare the relative magnitude of the change between morphological and behavioral traits, we replicated this analysis using the dimensionless relative rates of change in trait expression. We then determined whether there was senescence in these secondary sexual traits by testing the hypothesis that trait expression declines following their maximum expression. Finally, we introduced a novel peak-centering analysis, where the expressions of morphological traits and behaviors were related to male peak lekking effort, to test the hypothesis that trait expression depends on the individual timing of reproductive effort, independently from male age *per se*.

Material and Methods

Study Population

Five black grouse leks were monitored in Central Finland (ca. 62°15'N; 25°00'E) in 2002–2013. Each lek is the local main lek holding 5–40 territorial males. The age structure of our study populations was assumed to be natural, as local hunting societies have refrained from hunting on these leks and in their close surroundings. During the study period the local population density varied from 6.2 to 14.6 individuals per km^2 of woodland (autumn

wildlife triangle censuses, organized by Finnish Game and Fisheries Research Institute), which was consistent with the observed age structure and the total number of males in the studied winter flocks and leks (Online Fig. A1).

Morphological Data

Morphological data were collected on lek sites annually during January-March by catching black grouse with oat-baited walk-in traps (for methods, see Lebigre et al. 2012). Each bird captured for the first time was marked for future identification with a unique combination of an aluminum tarsus ring (with an individual serial number) and three colored plastic tarsus rings. Body mass (to the nearest 10 g), tarsus (to the nearest 0.1 mm) and lyre length (the longest tail feather from base to tip, to the nearest 1.0 mm) of each male were measured. If a male had lost his tail feathers and the new moulted feathers were still clearly growing, lyre length was considered as a missing data point. A sample of breast feathers was taken from each male and the reflectance of the feathers' blue chroma coloration was measured in laboratory (soon after the field season in 2002–2008 and collectively in 2011 for data from 2009–2011; not measured in 2012–2013, N = 7) with Avantes Spectrophotometer (GS 3100, EG & G Gamma Scientific, San Diego, CA; details in Siitari et al. 2007). Eye combs were recorded against a scale with a digital video camera and the total eye comb area (hereafter eye comb size) was measured from snapshots using ImageJ software v. 1.46r (Rasband 2012).

Behavioral Data

Behavioral data were collected at the study leks annually during the mating season (typically lasting 8 to 12 days in late April – early May). During this period each lek was

monitored daily approximately from 0300 to 0800 hours from a hide next to the lek (males also display to some extent before sunset, but copulations occur in the morning; Alatalo, Lebigre & Siitari, personal observations). Male behavior was categorized as rookooing, hissing (i.e. the two main vocal displays), fighting or inactive (details in Höglund et al. 1997) and the location (x-y coordinates) of all ringed males (all males holding central territories and overall > 90 % of the territorial males were ringed) on the lek were recorded at regular intervals. Time and location of all copulations, and the identity of male and female involved were also recorded. Lek attendance (proportional to the highest attending male on the same lek that year) and the center of each male's territory (median coordinates of observations) were calculated for all territorial males (see Alatalo et al. 1996). Similarly, the location of the lek center (median coordinates of all observations of all males) and the linear distance of each male's territory center from the lek center were calculated. The relative proportion of each behavior was calculated for each male, but as these behaviors are mutually exclusive, only fighting rate was used in the analyses, as it likely has the greatest impact on male mating success (Hämäläinen et al. 2012).

Male Age and Lifespan

All captured unringed males were aged as yearling or older according to their plumage characteristics (Helminen 1963). Only males captured for the first time as yearlings were included in the data, as older males (≥ 2 years old) cannot be reliably aged based on morphological traits (Helminen 1963). Including males with uncertain age in the analyses would thus hinder the accurate quantifications of the effect of age on trait expression. As male black grouse are philopatric to their lekking site, adult dispersal is rare (Caizergues and Ellison 2002; Lebigre et al. 2008) and because ringed males visiting our study leks have virtually 100 % probability of being observed, territorial males no longer observed

were assumed to have died, and their last observation either on the lek (for behavioural traits) or during captures (for morphological traits) was used to determine their lifespan.

Data Validation

The data consisted of records of morphological traits (body mass, lyre length, blue chroma, eye comb size) and lekking behavior (lek attendance, fighting rate, territory distance from the lek centre) for 164 male black grouse with known year of hatching (2001–2008) and known lifespan of 1 to 6 years (totaling 423 records, Online Table A1). For the analyses, ages 5 and 6 were pooled into a single age class, and average trait values were used for the 7 males that were 6 years old. In case of missing data from either age, the existing trait values were used. Complete cohorts were available for males hatched in 2001–2006 and 2008, but 2 of the 130 ringed males hatched in 2007 were still alive in spring 2013. Since only two males out of > 1200 ringed males hatched between 2000 and 2006 reached age 7, all males of the 2007 cohort were assumed not to survive after the lekking season 2013, and the whole 2007 cohort was included in the analyses. Cohorts hatched 2009 onwards were excluded because of large proportions (> 10 %) of individuals still alive in spring 2013.

Statistical Analyses

Linear mixed-effects models (R package *lme4* v. 0.999999-2, Bates et al. 2013) with Gaussian (for all morphological traits and square root transformed territory distance from the lek center) or binomial error distributions with logit link function (for lek attendance and fighting rate, coded as binomial denominators) were used to analyze the data. Parameters were estimated using maximum likelihood which is recommended instead of

restricted maximum likelihood in model averaging (Bartón 2013). As our data consisted of several measurements from the same individuals at different ages, individual identity (nested within the study site, as each male was observed only on a single study site) was included as a random effect in all the models (van de Pol and Verhulst 2006).

First, the general effects of age (years) and lifespan (years) on the expression of morphological traits (body mass, lyre length, blue chroma, eye comb size) and behavioral attributes (lek attendance, fighting rate, territory distance from the lek center) were quantified. Tarsus length was also analyzed as an invariant trait since it should not change after males' first year of life. The fixed effects of male age and lifespan, and their interaction were introduced to the model to determine whether the effect of age on trait expression differs across males with different lifespan. Potential senescence (Jones et al. 2008; Nussey et al. 2013), was taken into account by including quadratic age as a fixed effect. The interaction of quadratic age with lifespan was also introduced as a fixed effect to investigate possible life history differences between individuals. A binary fixed effect 'terminal event' (1 = last observation, 0 = not the last observation) and its interaction with age and quadratic age were also included to account for potential terminal investment, as this can affect the evidence of senescence (Rattiste 2004; Hammers et al. 2012). Finally, the year of hatching was used as a fixed effect to account for potential cohort effects (i.e. the long-term effect of natal environmental conditions on individual performance; e.g. Millon et al. 2011). Although male fighting rate and territory distance from the lek center can be related to lek size, we did not include lek size as a fixed effect in any of the models due to issues with model convergence. To directly compare the rate of age-specific change across different morphological and behavioral traits, the same analyses were carried out using dimensionless rates of change (estimated as the difference in trait values at subsequent ages divided by the trait value in the youngest age) as dependent variables.

Significant quadratic age effect may provide limited evidence of senescence since it might solely result from steep increase in trait expression in early life (Bouwhuis et al. 2009). Therefore, the maximum trait values were identified for each individual and the previous analysis was implemented again without quadratic age effects using these pruned post-peak trait datasets, where a significant negative relationship of age on trait expression would provide evidence of senescence.

Finally, to investigate how male black grouse express morphological and behavioral traits in relation to the timing of their reproductive effort, a peak-centering approach was applied by rescaling age according to male peak lekking effort (hereafter peak-centered age). This novel method was modified from a recent model aiming at separating within- and between-individual effects of age on individual performance (see van de Pol and Wright 2009, eq. 2). Peak-centered age was calculated by subtracting the age at which a male's lek attendance was highest (relative to other males on the same lek on the same year) and subsequently used as a fixed effect. Individual age at peak lekking effort (hereafter age at peak) and the quadratic term of peak-centered age were introduced as a fixed effects to express selective (dis)appearance of lekking males and to account for potential nonlinear age effects respectively. These models applied to each trait were then slightly modified by replacing the peak-centered age by the original age (see van de Pol and Wright 2009, eq. 3). In these modified models, the effect of age at peak expressed the difference between selective (dis)appearance and individual scheduling in trait expression, thereby enabling the estimation of the relative importance of these two processes (van de Pol and Wright 2009). Peak-centered age was calculated only for males that had $\geq$ 75 % lek attendance in their peak lekking effort year to exclude the males that were not territorial on the studied leks. As lek attendance was used to scale the peak-centered age, the peak-centering analysis was not conducted to lek attendance.

All analyses were performed with R 2.15.2 (R Development Core Team 2012). Model selection followed AIC-IT procedure (Burnham and Anderson 2002). Due to model uncertainty, model averaging was used to combine the effects of the best candidate models within $\Delta AIC_c \leq 7$ (Burnham et al. 2011; Grueber et al. 2011) with the R package *MuMIn* v. 1.9.13 (Bartón 2013). Variable significance could then be compared by the averaged coefficient estimates and standard errors and the relative importance of each variable (the sum of Akaike weights of the models in which the variable appeared). As *P*-values for linear mixed effects models are not provided in the R package *lme4* (Bates et al. 2013), the effect sizes with 95 % confidence intervals were calculated for all fixed effects to enable the comparison of the biological importance of the effects (Nakagawa and Cuthill 2007). Effect size described using Pearson's r values can be interpreted as "small", "medium" and "large" when ≥ 0.1, ≥ 0.3 and ≥ 0.5, respectively (Cohen 1988).

Results

Age-dependent Expression of Male Traits

For all traits, several candidate models had $\Delta AIC_c \leq 7$ and multimodel inference was required (Online Table A2). Overall, age contributed substantially to all models, with body mass, lyre length, blue chroma and eye comb size increasing with male age but in a non-linear fashion as indicated by the significant quadratic age effects (Table 1 a–d, Fig. 1 a–d).

The high relative importance and the positive interactions of age and lifespan and quadratic age and lifespan on body mass, lyre length and to some extent eye comb size indicated that long-lived males (i.e. lifespan ≥ 4 years) had lower age-dependent trait expressions and delayed maximum trait values (Table 1 a–d, Fig. 1 a–d). Moreover,

lifespan had a major contribution to the best candidate models as it had high relative importance for all morphological traits (range: 0.74–1.00).

Terminal investment explained a substantial amount of the variation in body mass and lyre length, as indicated by the positive interactions of age and terminal event on body mass and quadratic age and terminal event on lyre length, and their high relative importance (Table 1 a–b). These interactions were primarily due to greater increase in traits from age 1 to age 2 in males that died at 2 years old (Fig. 2 a–b). There was no evidence of terminal investment for blue chroma and eye comb size (Table 1 c–d). As expected and contrary to all other morphological traits, tarsus length was unrelated to male age, lifespan and their interactions (Table 1 e, Fig. 1 e).

Consistent with the morphological traits, age was the key determinant of the expression of all behavioral traits (Table 1 f–h). Specifically, lek attendance and fighting rate increased significantly with age and males defended their territories closer to the lek center as they got older (Fig. 1 f–h), and there was a significant negative quadratic effect of age on lek attendance. Long-lived males had lower age-specific lekking effort and delayed peak lekking effort as indicated by the substantial amount of variation in lek attendance and fighting rate explained by the interaction of age and lifespan and quadratic age and lifespan (Fig. 1 f–g). Positive interactions of quadratic age and terminal event on lek attendance and fighting rate indicated higher trait expression on last observation in... Lek attendance increased and fighting rate decreased when males were last observed on leks.

The analysis of dimensionless rates of change in trait values revealed that there was no overall major difference in the effects of male age and lifespan on the expression of males' morphological and behavioral traits (Online Tables A3 and A4, Fig. 2). More specifically, the rates of change were most rapid between ages 1 and 2 for all traits after which the change was slow. Eye comb size had the greatest relative age-spefic change (Fig 2 d).

Senescence

Across all traits, there was a strong negative age effect following the maximum trait expression (Online Tables A5 and A6, Fig. 3) with very little variation in theirs relative importance (range: 0.98–1.00, Online Table A6). Overall, the effect sizes of morphological and behavioral traits were similar. Male lifespan explained substantially less variation in trait values than in the previous analysis; the effects interactions of age and lifespan were overall limited and relative importance of lifespan ranged from 0.31 (eye comb size) to 1.00 (lek attendance). Age-dependent decrease it trait expression was further shaped by terminal investment; specifically, the interactions of age and terminal event indicated that the increase in body mass, lek attendance and fighting rate, and the decrease in territory distance from the lek center in the last observation were greatest in males that died young (Online Table A6 a, e–g, Fig. 3 a, e–g). Across all ages, body mass increased during the males' last breeding season.

Trait Expression in Relation to Peak Lekking Effort

There was substantial variation in the age at peak lekking effort among male black grouse (median 2, range 1–5). Body mass, lyre length and eye comb size increased towards the year of individual peak lekking effort and was higher in males that had their peak lekking effort at older age (Table 2 a, b, d, Fig. 4 a, b, d). In addition, the negative quadratic effect of peak-centered age on lyre length had high relative importance, suggesting that males had shorter lyres after the year of peak lekking effort. Blue chroma and tarsus length were unrelated to peak-centered age or age at peak (Table 2 c, e, Fig. 4 c, e).

Males fought more and defended their territories closer to the lek center with increasing peak-centered age, but fought less and defended territories further from the lek center after the year of peak lekking effort, as indicated by the quadratic peak-centered age effects (Table 2 f–g, Fig. 4 f–g). Overall, fighting rate was higher and distance from the lek center lower in males that had their peak effort at older ages.

Discussion

Our study shows that the overall variation in trait expression, on which sexual selection is acting, results from very different allocation strategies which can only be revealed using comprehensive longitudinal data. Indeed, we found that two strategies of trait expression co-occur in this black grouse population, with short-lived males generally having higher age-specific morphological and behavioral trait expression than long-lived males. Trait expression dynamics were also partly explained by terminal investment suggesting fine tuning of male investment in trait expression according to their perceived current and future condition. Even with terminal investment, there were clear consistent decline in trait values following the age of maximum expression indicating that senescence occurred in both morphological and behavioral traits. Furthermore, a novel peak-centering analysis indicated that the individual timing of lekking effort is a major driver of the age- and lifespan-related patterns in trait expression in male black grouse. Accounting for such effects is fundamental to better understand sexual selection and the maintenance of genetic variation, if the fitness payoffs of the two alternative allocation strategies differ and if such strategies are partly genetically determined.

The effects of age on trait expression

Consistent with the expectation that the expression of morphological and behavioral traits is constrained in young individuals (Curio 1983), we found that the greatest change in trait values occurred from yearlings to 2-year-old males. During the first six months of their life, male black grouse grow rapidly, increasing their body mass approximately 50-fold. Therefore, yearling males may need to allocate most of their limited resources to the growth of vital traits leaving limited resources for the expression of their ornaments. Such pattern has been reported in species with conspicuous secondary sexual traits (Nussey et al. 2009; Evans et al. 2011) and might play a role in mate choice through discrimination against young but active males that have not undergone viability selection (Manning 1985; Alatalo et al. 1991). These age-dependent patterns differed from male tarsus length, which reached its final length during the first year of life. Therefore, the age-dependent expression of other morphological traits and behaviors were not artifacts arising from increased overall body size with age.

All male behavioral traits were also age-dependent with the greatest change in the expression of these traits occurring during the transition from yearlings to 2-year-old males. Lekking is energetically costly (Vehrencamp et al. 1989; Siitari et al. 2007; Lebigre et al. 2013), and heavy individuals are more capable of handling these costs (McElligott et al. 2002; Hämäläinen et al. 2012; Lebigre et al. 2013). Thus, yearling male black grouse, being on average some 100 grams (ca. 10 %) lighter than older males, may not be able to sustain as high lek attendance as older males (Kervinen et al. 2012). Males defended their territories closer to the lek center as they aged, supporting the hypothesis that territory centrality is an honest cue of male quality and viability in lekking species (e.g. Höglund and Lundberg 1987; Kokko et al. 1998, 1999).

There was no major difference in rates of change in trait expression between different traits, and only the change in the size of red eye combs was substantially more age-dependent that of all the other traits. It is well established that eye combs and other

406 fleshy structures such as wattles are testosterone dependent in birds (black grouse:
407 Rintamäki et al. 2000, Siitari et al. 2007; see also Zuk et al. 1995, Mougeot et al. 2004).
408 Therefore, such substantially greater rate of increase in male eye combs might be explained
409 by the very large increase in male gonads and testosterone levels with age, especially from
410 yearlings to 2-year-old males (Rintamäki 2000).
411
412 *Life history differences in trait expression*
413
414 There were major differences in life histories in male black grouse as the magnitude of the
415 change in morphological and behavioral traits was strongly related to the interaction
416 between age and lifespan, indicating that long-lived males had consistently lower trait
417 values at ages 1 to 3 than males with shorter lifespan. Therefore, two strategies of trait
418 expression co-occur in this population and major survival costs on the timing of expression
419 might occur. This is a commonly predicted (Stearns 1992) but a less frequently empirically
420 shown life history pattern (see e.g. Candolin 2000), suggesting that high trait expression at
421 an early stage of life has survival costs (Kotiaho 2001). Specifically, long-lived males were
422 lighter, had shorter lyres and lower lek attendance as yearlings than short-lived males.
423 Although these results should be interpreted cautiously given the unknown fate of many
424 yearling males (Kervinen et al. 2012), they are consistent with previous studies
425 investigating age-dependence of life history traits (Bouwhuis et al. 2010), and secondary
426 sexual traits (Balbontín et al. 2011). Moreover, a number of studies have shown that
427 elevated reproductive rate is associated with reduced lifespan and, in some cases,
428 accelerated ageing (Kotiaho 2001; Hunt et al 2004). These results are even more
429 remarkable because random mortality due to predation may reduce the power to detect the
430 relationship between trait expression and lifespan. However, male mortality is highest in
431 black grouse during the weeks following the lekking season when their condition decline

substantially (Lebigre et al. 2013). Therefore, predation may drive the effect of lifespan on male trait expression if individuals' predation risks are related to their lek performance and their ability to sustain the costs of the lek display.

It is unclear whether such differences in reproductive scheduling are genetically and/or environmentally driven. Our analysis found cohort effects only in male body mass and blue chroma coloration, but not in other traits. Therefore, the natal environment had little effect on ornament expression in black grouse although they can have long-lasting effects on individual life histories and the variation in trait expression (Lindström 1999; Metcalfe and Monaghan 2001). However, further analyses are needed to disentangle the causes and also the consequences of life history differences in trait expression.

Terminal investment and senescence

Male reproductive strategies driven by sexual selection may lead to reduced lifespan because of the costs associated with the expression of sexually selected morphological and behavioral traits (Bonduriansky et al. 2008). Such reduction in lifespan is expected to reduce the magnitude of natural selection acting on late acting genes and hence increase the rate of ageing in males (Carranza & Pérez-Barbería 2007; Preston et al. 2011). However, the relationship between senescence and sexual selection may not be found in species where sexually selected traits are condition-dependent, because sexual selection may favor individuals that are better able to sustain the costs of reproduction early in life and reach maximum trait values later in life (Clutton-Brock 1988; Bonduriansky et al. 2008). As a result, senescence in secondary sexual traits and behavior is less frequently recorded in nature than senescence in life history traits (e.g. Hoikkala et al. 2008; Nussey et al. 2009; Lecomte et al. 2010; Balbontín et al. 2011). In black grouse, all morphological

and behavioral traits reached a maximum expression and subsequently declined with age; therefore, senescence does occur in black grouse.

Declines in traits did not continue linearly as body mass, lek attendance, fighting rate increased and territory distance from the lek center decreased during males' last lekking season. As reproductive effort is expected to increase when residual reproductive value decreases, this increased reproductive effort prior to disappearance suggests terminal investment (Williams 1966; Clutton-Brock 1984; Sadd et al. 1996; Velando et al. 2006). Effect sizes for the interaction of age and terminal event were stronger for behavioral traits suggesting that male black grouse were able to increase their reproductive effort but could not resist the physical decline as they aged (Williams 1957; Hamilton 1966; Kokko 1997). This might be because size and quality of structural ornaments are strongly related to male physiological condition during the moult, which occurs shortly after the lekking season. Behavioral traits are in this sense more flexible; males can adjust their lekking behavior according to their condition just prior to the mating season. Therefore, the costs of lekking are more likely to be seen in terms of reduced overwinter survival and reduced ornament expression the following spring than in male lekking effort.

Trait Expression in Relation to Peak Lekking Effort

Our last analysis, where the data was reanalyzed with peak-centered age, indicated strong congruence between maximum trait expression and the peak lekking effort. Males expressed higher trait values with increasing peak-centered age but the year of peak lekking effort tended to occur in the last year the male was alive, especially in short-lived males. This suggests that although males may be able to modulate their reproductive effort according to their current condition (see earlier), lekking might induce substantial fitness costs in terms of reduced survival with stronger fitness costs in short-lived males, which in

turn suggest that long-lived males are of high genetic quality as they not only have proven their viability but are also more likely to survive to the next autumn and to the next breeding season (Alatalo et al. 1991). Therefore, the costs of reproductive effort (i.e. lekking) may not only underpin the expression of ornaments (e.g. tail plume in Jackson's widow birds *Euplectes jacksoni*: Andersson 1994), but ultimately the temporal scheduling of reproductive effort, i.e. life history strategies.

Conclusions

Overall, this study shows that the expressions of morphological and behavioral traits in black grouse are strongly age-dependent but that these effects are not consistent across all sexually-selected traits. Furthermore, there are major differences in trait expression trajectories between short- and long-lived males. There was also evidence of both senescence in all traits and terminal investment particularly in behavioral traits. These complex interactions could explain the substantial variation observed in the sexually-selected traits in male black grouse but also in many other species with weaker sexual selection. This study shows that accurate quantification of the magnitude of sexual selection acting on male morphological and/or behavioral traits in this and other species requires accounting for the simultaneous effects of individual age, lifespan and fine-tuned investment in reproduction.

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Literature Cited

Alatalo, R. V., J. Höglund, and A. Lundberg. 1991. Lekking in the black grouse – a test of male viability. Nature 352:155–156.

Alatalo, R. V., J. Höglund, A. Lundberg, and W. J. Sutherland. 1992. Evolution of black grouse leks – female preferences benefit males in larger leks. Behavioral Ecology 3:53–59.

Alatalo, R. V., J. Höglund, A. Lundberg, P. T. Rintamäki, and B. Silverin. 1996. Testosterone and male mating success on the black grouse leks. Proceedings of the Royal Society B: Biological Sciences 263:1697–1702.

Andersson, M. 1994. Sexual selection. Princeton. Princeton University Press.

Balbontín, J., F. de Lope, I. G. Hermosell, T. A. Mousseau, and A. P. Møller. 2011. Determinants of age-dependent change in a secondary sexual character. Journal of Evolutionary Biology 24:440–448.

Bartón, K. 2013. Package 'MuMIn': Multi-model inference. R package version 1.9.13. http://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Bates, D. M., M. Maechler, and B. Bolker. 2013. Package 'lme4': Linear mixed-effects models using S4 classes. R package version 0.999999-2. http://cran.r-project.org/web/packages/lme4/lme4.pdf.

535 Bonduriansky, R., A. Maklakov, F. Zajitschek, and R. Brooks. 2008. Sexual selection,
536 sexual conflict and the evolution of ageing and life span. Functional Ecology
537 22:443–453.
538 Bouwhuis, S., A. Charmantier, S. Verhulst, and B. C. Sheldon. 2010. Individual variation
539 in rates of senescence: natal origin effects and disposable soma in a wild bird
540 population. Journal of Animal Ecology 79:1251–1261.
541 Bouwhuis, S., R. Choquet, B. C. Sheldon, and S. Verhulst. 2012. The forms and fitness
542 cost of senescence: Age-specific recapture, survival, reproduction, and reproductive
543 value in a wild bird population. American Naturalist 179:E15–E27.
544 Bouwhuis, S., B. C. Sheldon, S. Verhulst, and A. Charmantier. 2009. Great tits growing
545 old: selective disappearance and the architecture of reproductive senescence.
546 Proceedings of the Royal Society B: Biological Sciences 276:2769–2777.
547 Brooks, R., and D. J. Kemp. 2001. Can older males deliver the good genes? Trends in
548 Ecology & Evolution 16:308–313.
549 Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a
550 practical information-theoretic approach. 2nd ed. New York, Springer.
551 Burnham, K. P, D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and
552 multimodel inference in behavioral ecology: some background, observations, and
553 comparisons. Behavioural Ecology and Sociobiology 65:23–35.
554 Candolin, U. 2000. Changes in expression and honesty of sexual signaling over the
555 reproductive lifetime of sticklebacks. Proceedings of the Royal Society B: Biological
556 Sciences 267: 2425–2430.
557 Caizergues, A., and L. N. Ellison. 2002. Natal dispersal and its consequences in black
558 grouse *Tetrao tetrix*. Ibis 144:478–487.

559 Carranza, J., and F. J. Pérez-Barbería. 2007. Sexual selection and senescence: male size-
560 dimorphic ungulates evolved relatively smaller molars than females. American
561 Naturalist 170:370–380.
562 Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous
563 animals. American Naturalist 123:212–229.
564 Clutton-Brock, T. H. 1988. Reproductive success: studies of individual variation in
565 contrasting breeding systems. The University of Chicago Press, Chicago.
566 Clutton-Brock, T. H., and B. C. Sheldon. 2010. Individuals and populations: the role of
567 long-term, individual-based studies of animals in ecology and evolutionary biology.
568 Trends in Ecology & Evolution 25:562–573.
569 Cohen, J. 1988. Statistical power analysis for the behavioral sciences, 2nd ed. Erlbaum,
570 Hillsdale, NJ.
571 Coltman D. W., M. Festa-Bianchet, J. T. Jorgenson, and C. Strobeck. 2002. Age-dependent
572 sexual selection in bighorn rams. Proceedings of the Royal Society B: Biological
573 Sciences 269:165–172.
574 Curio, E. 1983. Why do young birds reproduce less well? Ibis 125:400–404.
575 Dugdale, H. L., L. C. Pope, C. Newman, D. W. MacDonald, and T. Burke. 2011. Age-
576 specific breeding success in a wild mammalian population: selection, constraint,
577 restraint and senescence. Molecular Ecology 20:3261–3274.
578 Evans, S. R., L. Gustafsson, and B. C. Sheldon. 2011. Divergent patterns of age-
579 dependence in ornamental and reproductive traits in the collared flycatcher.
580 Evolution 65:1623–1636.
581 Froy, H., R. A. Phillips, A. G. Wood, D. H. Nussey, and S. Lewis. 2013. Age-related
582 variation in reproductive traits in the wandering albatross: evidence for terminal
583 improvement following senescence. Ecology Letters 16:642–649.

584 Grueber, C. E., S. Nakagawa, R. J. Lawis, and I. G. Jamieson. 2011. Multimodel inference
585 in ecology and evolution: challenges and solutions. Journal of Evolutionary Biology
586 24:699–711.
587 Hämäläinen, A., R. V. Alatalo, C. Lebigre, H. Siitari, and C. D. Soulsbury. 2012. Fighting
588 behaviour as a correlate of male mating success in black grouse *Tetrao tetrix*.
589 Behavioral Ecology and Sociobiology 66:1577–1586.
590 Hamilton, W. D. 1966. The moulding of senescence by natural selection. Journal of
591 Theoretical Biology 12:12–45.
592 Hammers, M., D. S. Richardson, T. Burke, and J. Komdeur. 2012. Age-dependent terminal
593 declines in reproductive output in a wild bird. PLoS ONE 7:e40413.
594 Helminen, M. 1963. Composition of the Finnish populations of capercaillie, *Tetrao*
595 *urogallus*, and black grouse, *Lyrulus tetrix*, in the autumns of 1952–1961, as revealed
596 by a study of wings. Riistatieteellisiä Julkaisuja 8:142–149.
597 Höglund, J., R. V. Alatalo, A. Lundberg, and O. Rätti. 1994. Context-dependent effects of
598 tail-ornament damage on mating success in black grouse. Behavioral Ecology 5:182–
599 187.
600 Höglund, J., T. Johansson, and C. Pelabon. 1997. Behaviourally mediated sexual selection:
601 Characteristics of successful male black grouse. Animal Behaviour 54:255–264.
602 Höglund, J., and A. Lundberg. 1987. Sexual selection in a monomorphic lek-breeding bird:
603 correlates of male mating success in the great snipe *Gallinago media*. Behavioral
604 Ecology 21:211–216.
605 Hoikkala, A., M. Saarikettu, J. S. Kotiaho, and J. O. Liimatainen. 2008. Age-related
606 decrease in male reproductive success and song quality in *Drosophila montana*.
607 Behavioral Ecology 19: 94–99.

608 Hovi, M., R. V. Alatalo, J. Höglund, A. Lundberg, and P. T. Rintamäki. 1994. Lek center
609 attracts black grouse females. Proceedings of the Royal Society B: Biological
610 Sciences 258:303–305.
611 Hunt J., R. Brooks, M. Jennions, M. Smith, C. Bentsen, and L. Bussiere. 2004. High-
612 quality male field crickets invest heavily in sexual display but die young. Nature
613 432:1024–1027.
614 Jones, O. R., J.-M. Gaillard, S. Tuljapurkar, J. S. Alho, K. B. Armitage, P. H. Becker, P.
615 Bize, J. Brommer, A. Charmantier, M. Charpentier, T. H. Clutton-Brock, F. S.
616 Dobson, M. Festa-Bianchet, L. Gustafsson, H. Jensen, C. G. Jones, B.-G. Lilland, R.
617 McCleery, J. Merilä, P. Neuhaus, M. A. C. Nicoll, K. Norris, M. K. Oli, J.
618 Pemberton, H. Pietiäinen, T. H. Ringsby, A. Roulin, B. E. Saether, J. M. Setchell, B.
619 C. Sheldon, P.M. Thompson, H. Weimerskirch, E. J. Wickings, and T. Coulson.
620 2008. Senescence rates are determined by ranking on the fast-slow life-history
621 continuum. Ecology Letters 11:664–673.
622 Kervinen, M., R. V. Alatalo, C. Lebigre, H. Siitari, and C. D. Soulsbury. 2012.
623 Determinants of yearling male lekking effort and mating success in black grouse
624 (*Tetrao tetrix*). Behavioral Ecology 23:1209–1217.
625 Kokko, H. 1997. Evolutionarily stable strategies of age-dependent sexual advertisement.
626 Behavioral Ecology and Sociobiology 41:99–107.
627 Kokko, H., J. Lindström, R. V. Alatalo, and P. T. Rintamäki. 1998. Queuing for territory
628 positions in the lekking black grouse (*Tetrao tetrix*). Behavioral Ecology 9:376-383.
629 Kokko, H., P. T. Rintamäki, R. V. Alatalo, J. Höglund, E. Karvonen E, and A. Lundberg.
630 1999. Female choice selects for lifetime lekking performance in black grouse males.
631 Proceedings of the Royal Society B: Biological Sciences 266:2109–2115.
632 Kotiaho, J. S. 2001. Costs of sexual traits: a mismatch between theoretical considerations
633 and empirical evidence. Biological Reviews 76:365–376.

634 Lebigre, C., R. V. Alatalo, H. E. Forss, and H. Siitari. 2008. Low levels of relatedness on
635 black grouse leks despite male philopatry. Molecular Ecology. 17:4512–4521.
636 Lebigre, C., R. V. Alatalo, J. Kilpimaa, V. Staszewski, and H. Siitari. 2012. Leucocyte
637 counts variation and measures of male fitness in the lekking black grouse. Journal of
638 Ornithology 153:95–102.
639 Lebigre, C., R. V. Alatalo, and H. Siitari. 2013. Physiological costs enforce the honesty of
640 lek display in the black grouse (*Tetrao tetrix*). Oecologia 172:983-993.
641 Lecomte, V. J., G. Sorci, S. Cornet, A. Jaeger, B. Faivre, E. Arnoux, M. Gaillard, C.
642 Trouve, D. Besson, O. Chastel, and H. Weimerskirch. 2010. Patterns of aging in the
643 long-lived wandering albatross. Proceedings of the National Academy of Sciences of
644 the United States of America 107:6370–6375.
645 Lindström, J. 1999. Early development and fitness in birds and mammals. Trends in
646 Ecology & Evolution 14:342–348.
647 Mainguy, J., and S. D. Côté. 2008. Age- and state-dependent reproductive effort in male
648 mountain goats, *Oreamnos americanus*. Behavioral Ecology and Sociobiology
649 62:935–943.
650 Manning, J. T. 1985. Choosy females and correlates of male age. Journal of Theoretical
651 Biology 116:349–354.
652 Massot, M., J. Clobert, L. Montes-Poloni, C. Haussy, J. Cubo, and S. Meylan. 2011. An
653 integrative study of ageing in a wild population of common lizards. Functional
654 Ecology 25:848–858.
655 McElligott, A. G., R. Altwegg, and T. J. Hayden. 2002. Age-specific survival and
656 reproductive probabilities: evidence for senescence in male fallow deer (*Dama*
657 *dama*). Proceedings of the Royal Society B: Biological Sciences 269:1129–1137.
658 Metcalfe, N. B., and P. Monaghan. 2001. Compensation for a bad start: grow now, pay
659 later? Trends in Ecology & Evolution 16:254–260.

660 Millon, A., S. J. Petty, B. Little, and X. Lambin. 2011. Natal conditions alter age-specific
661 reproduction but not survival or senescence in a long-lived bird of prey. Journal of
662 Animal Ecology 80:968–975.
663 Monaghan, P., A. Charmantier, D. H. Nussey, and R. E. Ricklefs. 2008. The evolutionary
664 ecology of senescence. Functional Ecology 22:371–378.
665 Mougeot F., J. R. Irvine, L. Seivwright, S. M. Redpath, and S. Piertney. 2004.
666 Testosterone, immunocompetence, and honest sexual signaling in male red grouse.
667 Behavioral Ecology 15:930–937.
668 Nakagawa, S., and I. C. Cuthill. 2007. Effect size, confidence interval and statistical
669 significance: a practical guide for biologists. Biological Reviews 82:591–605.
670 Nussey, D. H, H. Froy, J.-F. Lemaitre, J.-M. Gaillard, and S. N. Austad. 2013. Senescence
671 in natural populations of animals: Widespread evidence and its implications for bio-
672 gerontology. Ageing Research Reviews 12:214– 225.
673 Nussey, D. H., L. E. B. Kruuk, A. Morris, M. N. Clements, J. M. Pemberton, and T. H.
674 Clutton-Brock. 2009. Inter- and intrasexual variation in aging patterns across
675 reproductive traits in a wild red deer population. American Naturalist 174: 342–357.
676 Preston, B. T., M. Saint Jalme, Y. Hingrat, F. Lacroix, and G. Sorci. 2011. Sexually
677 extravagant males age more rapidly. Ecology Letters 14: 1017-1024.
678 R Development Core Team. 2012. R: A language and environment for statistical
679 computing. R Foundation for Statistical Computing. Vienna, Austria.
680 Rasband, W. S. 2012. ImageJ (v. 1.46r). U. S. National Institutes of Health. Bethesda,
681 Maryland. USA. URL: http://imagej.nih.gov/ij/.
682 Rattiste, K. 2004. Reproductive success in presenescent common gulls (*Larus canus*): the
683 importance of the last year of life. Proceedings of the Royal Society B: Biological
684 Sciences 271: 2059–2064.

685 Rebke, M., T. Coulson, P. H. Becker, and J. W. Vaupel. 2010. Reproductive improvement
686 and senescence in a long-lived bird. Proceedings of the National Academy of
687 Sciences of the USA 107:7841–7846.
688 Reznick, D., L. Nunney, and A. Tessier. 2000. Big houses, big cars, superfleas and the
689 costs of reproduction. Trends in Ecology & Evolution 15:421–425.
690 Rintamäki, P. T., J. Höglund, E. Karvonen, R. V. Alatalo, N. Björklund, A. Lundberg, O.
691 Rätti, and J. Vouti. 2000. Combs and sexual selection in black grouse (*Tetrao tetrix*).
692 Behavioral Ecology. 5:465–471.
693 Sadd, B., L. Holman, H. Armitage, F. Lock, R. Marland, and M. T. Siva-Jothy. 1996.
694 Modulation of sexual signalling by immune challenged male mealworm beetles
695 (*Tenebrio molitor*, L.): evidence for terminal investment and dishonesty. Journal of
696 Evolutionary Biology 19:321–325.
697 Siitari, H., R. V. Alatalo, P. Halme, K. L. Buchanan, and J. Kilpimaa. 2007. Color signals
698 in the black grouse (*Tetrao tetrix*): Signal properties and their condition dependency.
699 American Naturalist 169:S81–S92.
700 Stearns, S. C. 1992. Evolution of life histories. Oxford. Oxford University Press.
701 van de Pol, M., and S. Verhulst. 2006. Age-dependent traits: a new statistical model to
702 separate within- and between individual effects. American Naturalist 167:765–773.
703 van de Pol, M., and J. Wright. 2009. A simple method for distinguishing within- versus
704 between-subject effects using mixed models. Animal Behaviour 77:753–758.
705 Vande Velde, L., P. Silvestre, D. Damiens, and H. Van Dyck. 2011. Male reproductive
706 investment relative to age and flight behaviour in the monandrous butterfly *Pararge*
707 *aegeria*. Behavioral Ecology and Sociobiology 66:347–359.
708 Vehrencamp, S. L., J. W. Bradbury, and R. M. Gibson. 1989. The energetic cost of display
709 in male sage grouse. Animal Behaviour 38:885–896.

Velando, A., H. Drummond, and R. Torres. 2006. Senescent birds redouble reproductive effort when ill: confirmation of the terminal investment hypothesis. Proceedings of the Royal Society B: Biological Sciences 273:1443–1448.

Williams, G. C. 1957. Pleiotropy, natural selection and the evolution of senescence. Evolution 11:398–411.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100:687–690.

Zahavi, A. 1975. Mate selection—selection for a handicap. Journal of Theoretical Biology 53:205–214.

Zuk, M., T. S. Johnsen, and T. Maclarty. 1995. Endocrine-immune interactions, ornaments and mate choice in red jungle fowl. Proceedings of the Royal Society B: Biological Sciences 260:205–210.

Tables

Table 1. The relative importance, coefficient estimates, standard errors (SE) and effect sizes (Pearson's r with 95% CI) of the fixed effects of age, age^2, lifespan (LS), terminal event (TE), cohort and the relevant interactions (denoted by colons) on morphological (a–e) and behavioral traits (f–h) after model averaging. Statistically significant effects (95 % CI does not overlap with 0) are in bold.

Model	Parameter	Relative importance	Estimate	SE	Effect size, r (95 % CI)
a) Body mass, n = 164	(Intercept)	—	1271.66	11.45	—
id:site var = 1310	**Age**	**1.00**	**90.10**	**13.71**	**0.31 (0.21, 0.39)**
residual var = 1296	**Age^2**	**1.00**	**−234.57**	**35.08**	**−0.31 (−0.39, −0.22)**
	LS	1.00	−0.86	16.54	−0.00 (−0.10, 0.09)
	TE	1.00	21.89	13.58	0.08 (−0.18, 0.17)
	Cohort	0.76	—	—	—
	Age:LS	**1.00**	**103.14**	**38.02**	**0.13 (0.04, 0.22)**
	Age:TE	**1.00**	**80.32**	**27.90**	**0.14 (0.04, 0.23)**
	Age^2:LS	**1.00**	**120.16**	**27.52**	**0.21 (0.11, 0.30)**
	Age^2:TE	0.61	−44.13	25.18	−0.09 (−0.18, 0.01)
b) Lyre length, n = 163	(Intercept)	—	222.55	0.88	—

id:site var = 35.95	**Age**	**1.00**	**35.16**	**2.93**	**0.55 (0.47, 0.62)**
residual var = 54.05	**Age^2**	**1.00**	**−67.95**	**8.35**	**−0.41 (−0.49, −0.31)**
	LS	1.00	−6.57	3.40	−0.10 (−0.21, 0.00)
	TE	1.00	0.38	3.13	0.01 (−0.10, 0.11)
	Age:LS	0.64	13.57	8.13	0.09 (−0.02, 0.20)
	Age:TE	0.71	11.10	5.97	0.10 (−0.01, 0.20)
	Age^2:LS	**1.00**	**38.65**	**5.76**	**0.34 (0.24, 0.43)**
	Age^2:TE	**0.70**	**10.96**	**5.39**	**0.11 (0.00, 0.21)**
c) Blue chroma, n = 161	(Intercept)	—	26.81	0.42	—
id:site var = 0.37	**Age**	**0.90**	**1.14**	**0.54**	**0.14 (0.01, 0.27)**
residual var = 4.55	**Age^2**	**0.83**	**−1.90**	**0.95**	**−0.14 (−0.26, −0.00)**
	LS	0.76	−0.88	0.65	−0.09 (−0.22, 0.04)
	TE	0.61	0.33	0.54	0.04 (−0.09, 0.17)
	Cohort	1.00	—	—	—
	Age:LS	**0.59**	**−2.42**	**1.06**	**−0.15 (−0.28, −0.02)**
	Age:TE	0.21	−0.10	1.05	−0.01 (−0.14, 0.13)
	Age^2:LS	0.15	0.43	1.29	0.02 (−0.11, 0.15)
	Age^2:TE	0.12	−0.31	1.06	−0.02 (−0.15, 0.11)
d) Eye comb size, n = 162	(Intercept)	—	3.78	0.10	—
id:site var = 0.25	**Age**	**1.00**	**2.56**	**0.18**	**0.66 (0.59, 0.72)**
residual var = 0.79	**Age^2**	**1.00**	**−2.13**	**0.49**	**−0.26 (−0.36, −0.14)**
	LS	0.74	−0.29	0.22	−0.08 (−0.20, 0.04)
	TE	0.44	0.01	0.18	0.00 (−0.12, 0.12)
	Age:LS	0.20	0.11	0.57	0.01 (−0.11, 0.13)
	Age:TE	0.15	0.34	0.40	0.05 (−0.07, 0.17)
	Age^2:LS	**0.59**	**1.18**	**0.55**	**0.13 (0.01, 0.25)**
	Age^2:TE	0.12	0.09	0.48	0.01 (−0.11, 0.13)
e) Tarsus length, n = 164	(Intercept)	—	59.39	0.17	—
id:site var = 0.66	Age	0.33	0.11	0.17	0.04 (−0.07, 0.14)
residual var = 1.04	Age^2	0.20	−0.04	0.20	−0.01 (−0.12, 0.10)
	LS	0.25	0.15	0.20	0.04 (−0.06, 0.15)
	TE	**0.93**	**0.29**	**0.13**	**0.12 (0.01, 0.22)**
	Cohort	0.23	−1.76	1.12	−0.08 (−0.19, 0.02)
	Age^2:TE	0.04	−0.07	0.25	−0.01 (−0.09, 0.12)
f) Lek attendance, n = 164	(Intercept)	—	1.85	0.13	—
id:site var = 1.97	**Age**	**1.00**	**1.86**	**0.17**	**0.37 (0.30, 0.44)**
residual var = 1.00	**Age^2**	**1.00**	**−7.60**	**0.43**	**−0.55 (−0.61, −0.49)**
	LS	1.00	−0.56	0.34	−0.06 (−0.14, 0.01)
	TE	**1.00**	**1.01**	**0.13**	**0.28 (0.20, 0.35)**
	Age:LS	**1.00**	**3.25**	**0.38**	**0.31 (0.24, 0.38)**
	Age:TE	0.47	0.57	0.45	0.05 (−0.03, 0.12)
	Age^2:LS	**1.00**	**5.58**	**0.39**	**0.48 (0.41, 0.54)**
	Age^2:TE	**0.76**	**0.70**	**0.28**	**0.09 (0.02, 0.17)**
g) Fighting rate, n =164	(Intercept)	—	−1.15	0.07	—
id:site var = 0.44	**Age**	**1.00**	**1.00**	**0.20**	**0.33 (0.20, 0.44)**
residual var = 1.00	Age^2	1.00	−0.18	0.31	−0.04 (−0.17, 0.10)
	LS	0.90	−0.44	0.24	−0.12 (−0.25, 0.01)
	TE	**1.00**	**−0.49**	**0.15**	**−0.22 (−0.34, −0.08)**
	Age:LS	**0.86**	**−0.99**	**0.38**	**−0.18 (−0.30, −0.04)**
	Age:TE	0.34	−0.21	0.32	−0.05 (−0.18, 0.09)
	Age^2:LS	0.23	0.04	0.28	0.01 (−0.12, 0.14)

	Age^2:TE	**1.00**	**0.68**	**0.22**	**0.21 (0.08, 0.33)**
h) Distance*, n = 164	(Intercept)	—	4.33	0.11	—
id:site var = 0.67	**Age**	**1.00**	**−1.25**	**0.30**	**−0.26 (−0.37, −0.14)**
residual var = 0.99	Age^2	0.62	0.38	0.40	0.06 (−0.06, 0.19)
	LS	0.56	0.25	0.37	0.04 (−0.08, 0.17)
	TE	0.45	0.17	0.25	0.04 (−0.08, 0.17)
	Age:LS	0.38	0.83	0.48	0.11 (−0.02, 0.23)
	Age:TE	0.11	−0.03	0.41	−0.01 (−0.13, 0.12)
	Age^2:LS	0.06	−0.02	0.65	−0.00 (−0.13, 0.12)
	Age^2:TE	0.06	0.23	0.52	0.03 (−0.10, 0.15)

Note: Individual identity nested in study site was fitted as a random effect in all models. Parameter values of blue chroma were rescaled by multiplying the original values by 100 to obtain more informative coefficient estimates and standard errors. Random effects are represented as id:site and residual variances in the full model. * Territory distance from the lek center (sqrt transformed).

Table 2. The expression of morphological (a–e) and behavioral traits (f–g) with their coefficient estimates, standard errors (SE) and effect sizes (Pearson's r with 95 % CI) in relation to individual scheduling of male reproductive effort. Statistically significant effects (95 % CI does not overlap with 0) are in bold.

Model	Parameter	Estimate	SE	Effect size, r (95 % CI)
a) Body mass, n = 124	Intercept	1179.42	10.72	—
id:site variance = 1090.98	**Peak-centered age**	**40.95**	**2.67**	**0.67 (0.60, 0.73)**
residual variance = 2146.47	Peak-centered age^2	−2.43	1.31	−0.10 (−0.22, 0.01)
	Age at peak	**28.64**	**4.12**	**0.38 (0.27, 0.47)**
	Age at peak vs. peak-centered age	**−12.31**	**3.95**	**−0.18 (−0.29, −0.06)**
b) Lyre length, n = 123	Intercept	191.30	2.33	—
id:site variance = 6.44	**Peak-centered age**	**10.84**	**0.91**	**0.66 (0.57, 0.72)**
residual variance = 192.35	**Peak-centered age^2**	**−0.88**	**0.37**	**−0.17 (−0.30, −0.03)**
	Age at peak	**9.87**	**0.92**	**0.62 (0.52, 0.69)**
	Age at peak vs. peak-centered age	−0.97	1.05	−0.07 (−0.21, 0.08)
c) Blue chroma, n = 121	Intercept	25.15	0.48	—
id:site variance = 1.58	Peak-centered age	−0.00	0.13	−0.00 (−0.13, 0.12)
residual variance = 2.82	Peak-centered age^2	0.02	0.06	0.02 (−0.10, 0.15)
	Age at peak	−0.15	0.18	−0.05 (−0.18, 0.08)
	Age at peak vs. peak-centered age	−0.15	0.17	−0.05 (−0.18, 0.07)
d) Eye comb size, n = 123	Intercept	1.93	0.20	—
id:site variance = 0.18	**Peak-centered age**	**0.89**	**0.06**	**0.72 (0.64, 0.77)**
residual variance = 1.10	Peak-centered age^2	−0.01	0.03	−0.03 (−0.17, 0.10)
	Age at peak	**0.72**	**0.08**	**0.54 (0.44, 0.63)**
	Age at peak vs. peak-centered age	**−0.17**	**0.07**	**−0.16 (−0.29, −0.03)**
e) Tarsus length, n = 124	Intercept	59.28	0.25	—
id:site variance = 0.64	Peak-centered age	0.10	0.06	0.09 (−0.02, 0.20)

residual variance = 1.13	Peak-centered age^2	−0.01	0.03	−0.02 (−0.13, 0.10)
	Age at peak	0.04	0.10	0.02 (−0.09, 0.14)
	Age at peak vs. peak-centered age	−0.06	0.09	−0.04 (−0.15, 0.08)
f) Fighting rate, n = 124	Intercept	−1.46	0.15	—
id:site variance = 0.36	Peak-centered age	0.06	0.03	0.14 (−0.01, 0.27)
residual variance = 1.00	**Peak-centered age^2**	**−0.09**	**0.02**	**−0.41 (−0.51, −0.28)**
	Age at peak	**0.14**	**0.06**	**0.18 (0.04, 0.31)**
	Age at peak vs. peak-centered age	0.08	0.06	0.19 (−0.05, 0.24)
g) Distance*, n = 124	Intercept	4.81	0.25	—
id:site variance = 0.52	**Peak-centered age**	**−0.33**	**0.09**	**−0.25 (−0.37, −0.12)**
residual variance = 1.01	**Peak-centered age^2**	**0.10**	**0.04**	**0.18 (0.04, 0.30)**
	Age at peak	**−0.34**	**0.09**	**−0.24 (−0.37, −0.11)**
	Age at peak vs. peak-centered age	−0.01	0.11	−0.01 (−0.14, 0.13)

Notes: Age at peak vs. peak-centered age difference expresses the relative importance of these effects (see Material and Methods). Nonsignificant quadratic terms of peak-centered age were excluded from the final models, and values of the excluded variables refer to the step before their exclusion. Individual identity nested in study site was fitted as a random effect in all models. Parameter values of blue chroma were rescaled by multiplying the original values by 100 to obtain more informative coefficient estimates and standard errors. Random effects are presented as id:site and residual variances in the final model. * Territory distance from the lek center (sqrt transformed).

Figure Legends

Figure 1. Cross-sectional patterns of the observed age-specific expression (mean ± SE) of morphological traits (a–e) and behavioral attributes (f–g) for male black grouse of known age and lifespan (1 to 6 years; 5 and 6 pooled into class 5). Lines connecting the observed values have been added to aid visualization.

Figure 2. The relative rate of change in trait expression between subsequent years. The change was most rapid between ages 1 and 2, but there was no major differences in the magnitude of the change between different traits.

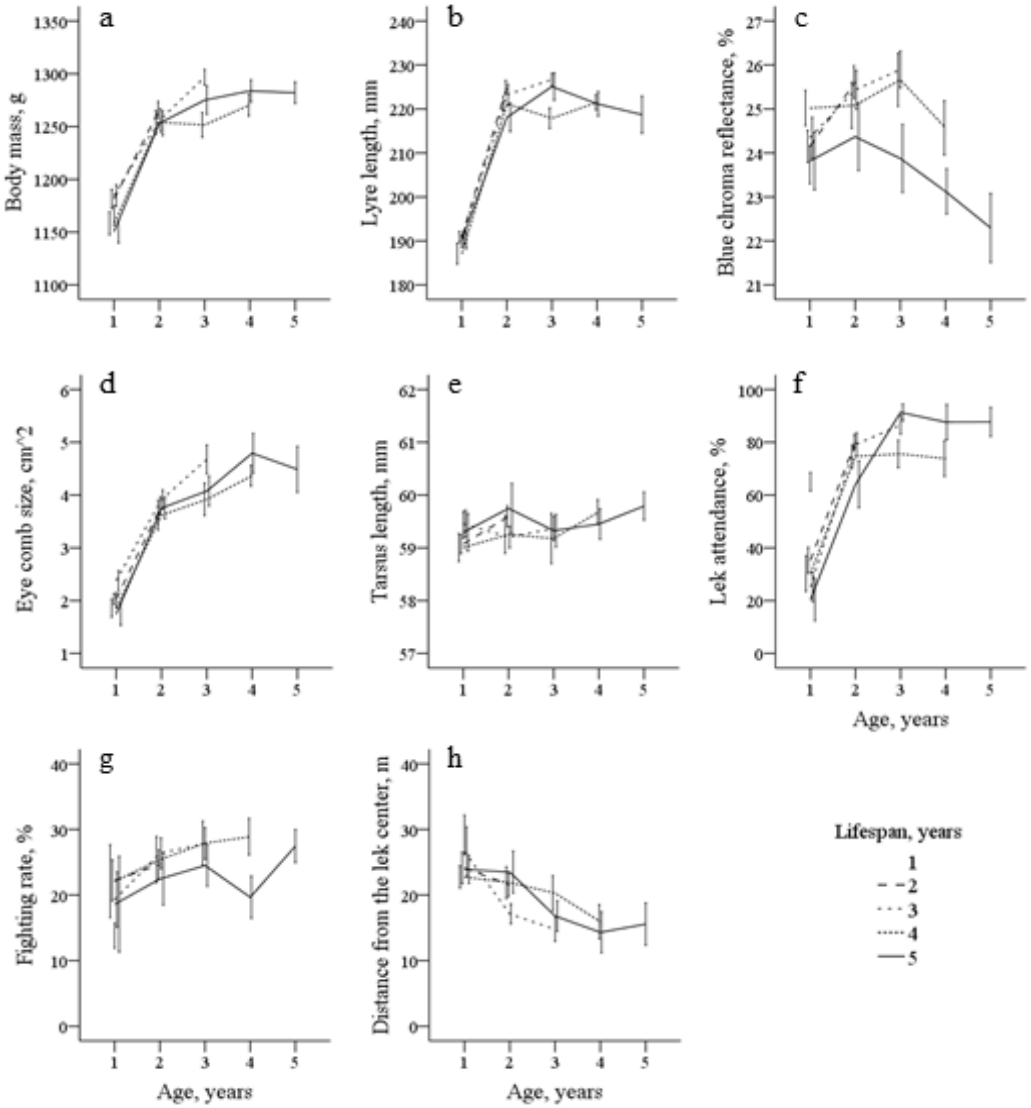
Figure 3. Trait expression (mean ± SE) after the individual trait maxima. Year 0 represents the observation of the maximum trait expression of the given trait of a given individual.

761 Grey squares represent observations of terminal events and black circles observations from
762 other years.
763
764 **Figure 4.** Cross-sectional patterns of the observed expression (mean ± SE) of
765 morphological (a–e) and behavioral traits (f–g) in relation to year of male peak lekking
766 effort for male black grouse with known age at peak (1 to 6 years; 5 and 6 are pooled into
767 class 5). Peak-centered age of 0 is the year when a male's lek attendance was highest
768 during its lifespan. Lines connecting the observed values have been added to aid
769 visualization.
770

771 **Figures**

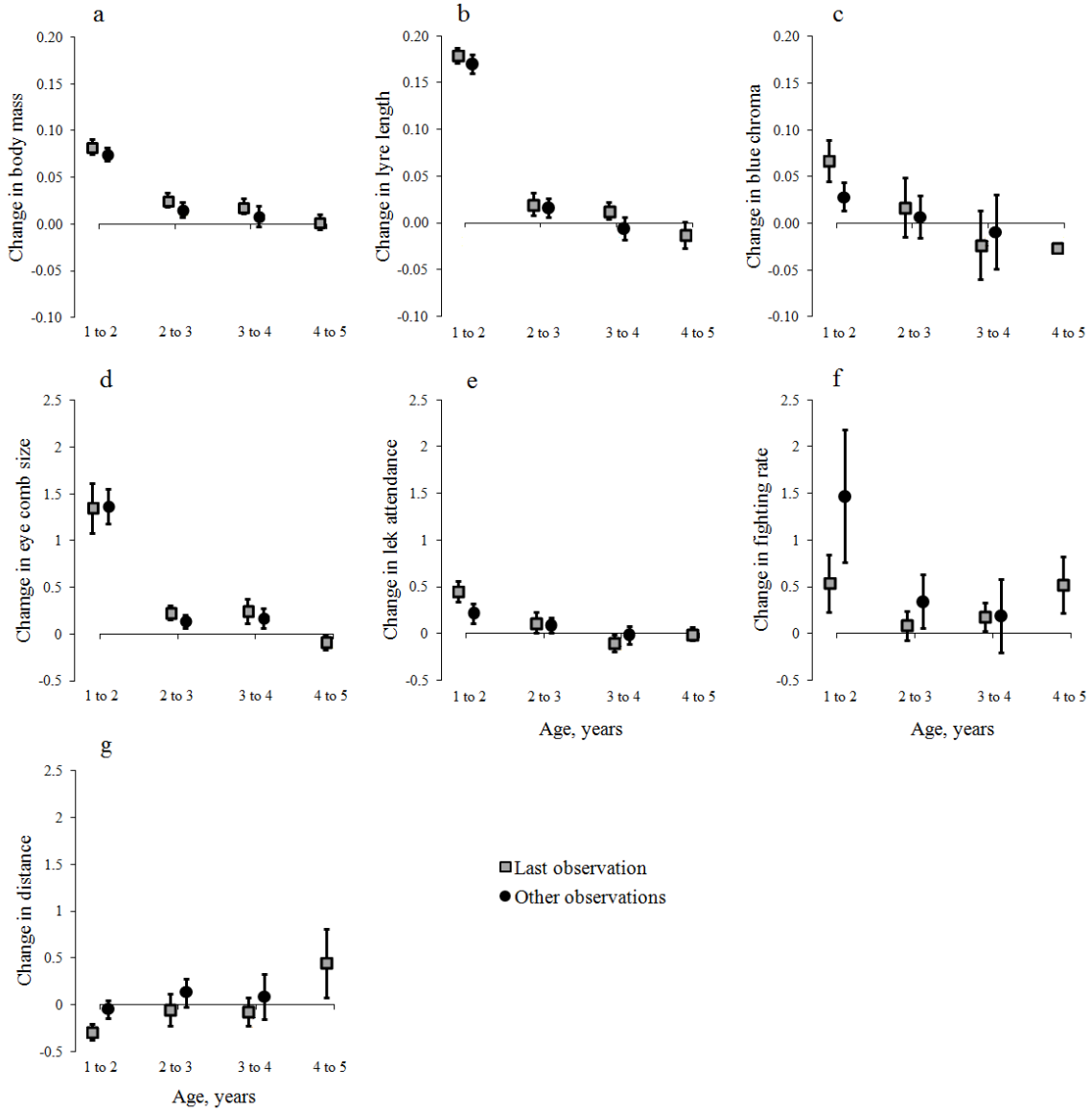
772

773 **Figure 1.**



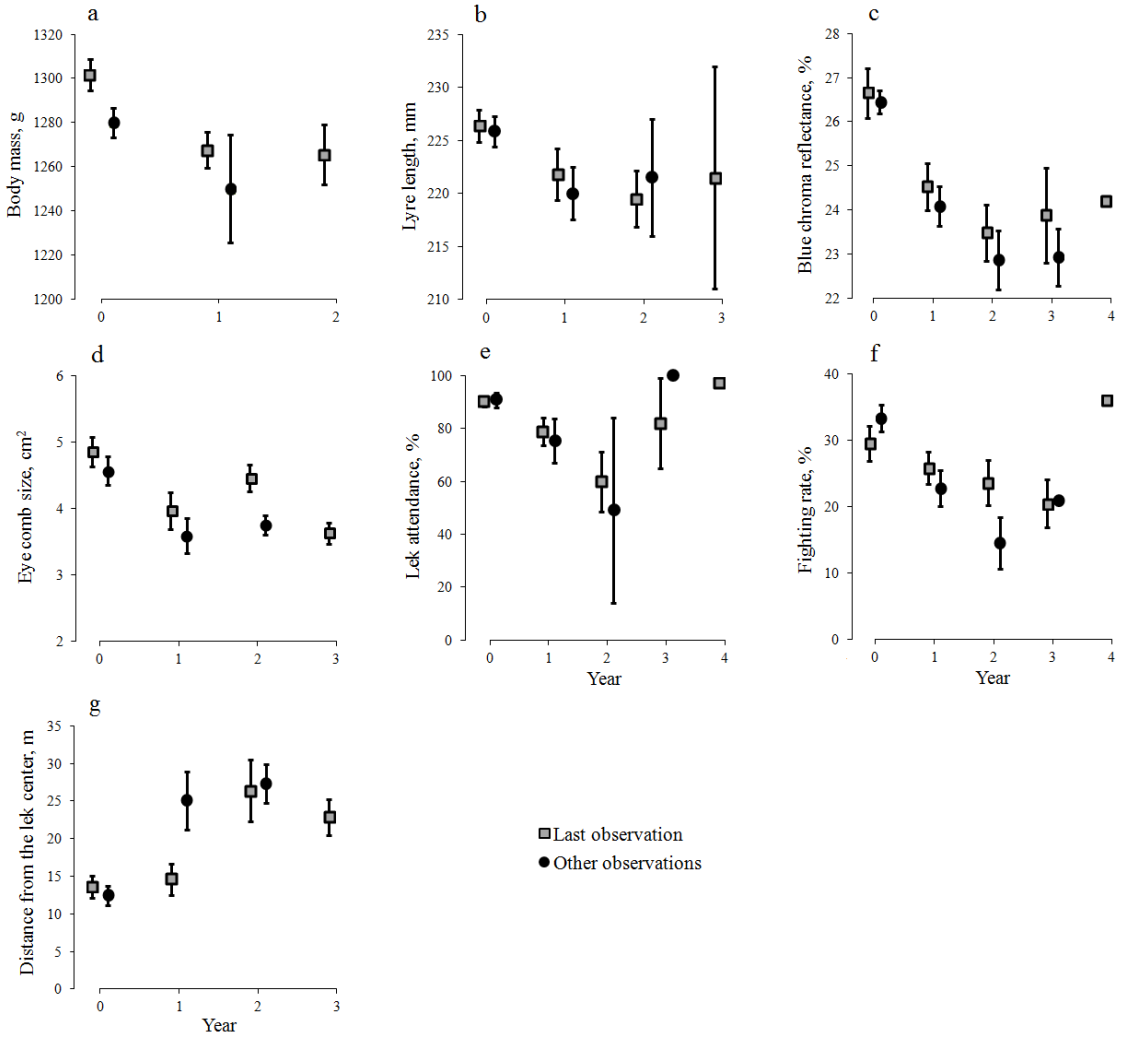
774

775 **Figure 2.**



776

777 **Figure 3.**



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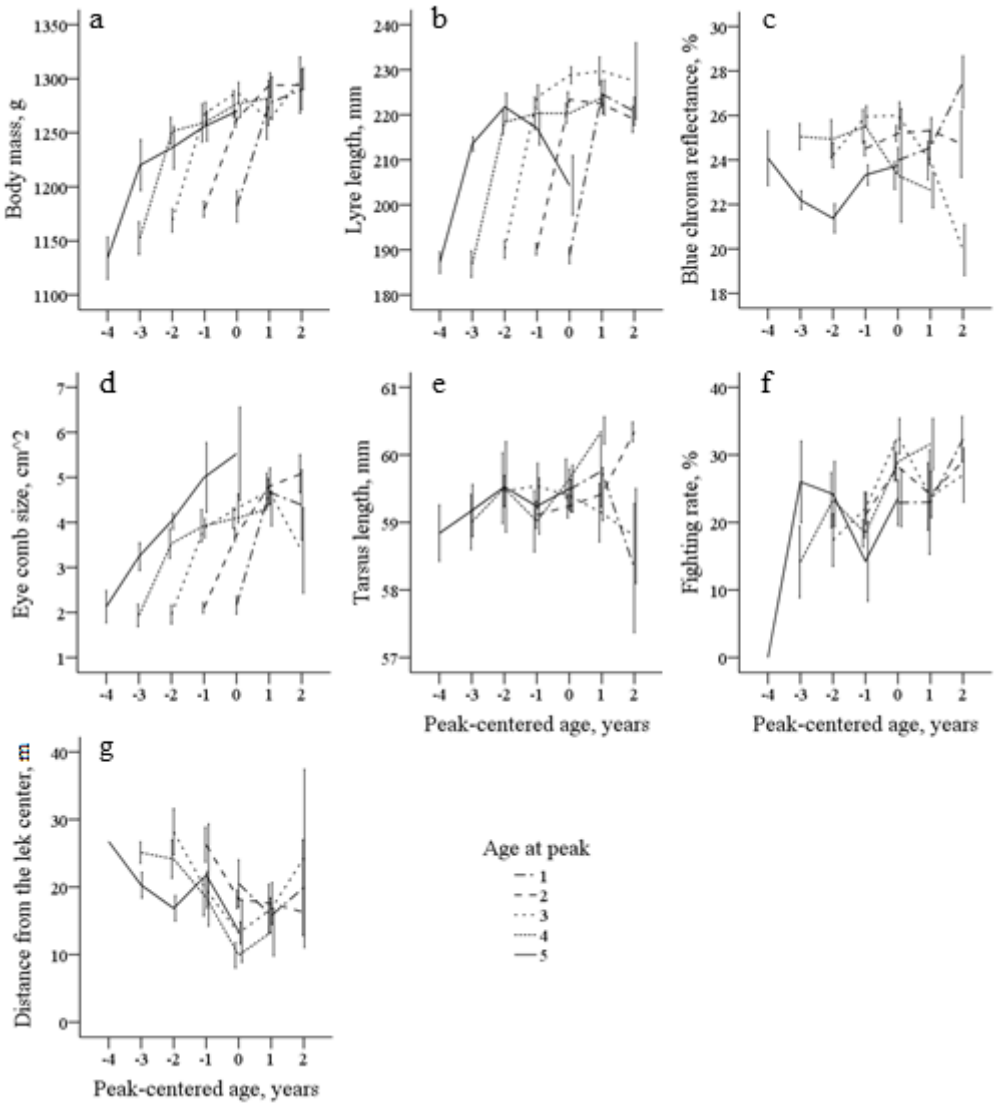
779

780 **Figure 4.**



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Online appendix A

Online Table A1. Number of data points of each lifespan-age class used in the analyses. Ages 5 and 6 were pooled into a single age class (≥5), as only 7 males survived to age 6. In these 7 cases the average trait values of the individual at ages 5 and 6 were used. In case of missing data from either age, the existing trait values were used, respectively. Attendance = lek attendance, fighting = fighting rate, Distance = territory distance from the lek center.

Lifespan	Age	Body mass	Lyre length	Blue chroma	Eye comb size	Tarsus length	Attendance	Fighting	Distance
1	1	34	33	31	32	34	38	38	38
2	1	51	52	51	51	52	57	22	23
	2	46	46	44	45	46	57	57	57
3	1	36	35	33	34	35	35	13	13
	2	29	28	29	29	29	30	27	27
	3	32	29	31	31	32	35	33	33
4	1	25	25	25	24	25	21	11	11
	2	20	19	20	20	19	20	18	18
	3	16	16	16	15	16	20	19	19
	4	21	20	20	20	21	21	18	18
≥5	1	13	14	13	13	14	13	4	4
	2	13	13	13	13	13	13	11	11
	3	12	12	12	12	12	13	13	13
	4	12	12	12	12	12	12	11	11
	≥5	10	10	9	10	10	13	13	11

Online Table A2. A suite of best candidate models ($\Delta AIC_c \leq 7$) predicting the expression of morphological (a–e) and behavioral (f–h) traits with the log-likelihood estimate, AIC_c values, ΔAIC_c, model weights and evidence ratios (ER).

Analysis	Rank	Model	LogLik	AIC_c	ΔAIC_c	Weight	ER
a) Body mass	1	A + A^2 + LS + TE + C + A:LS + A:TE + A^2:LS + A^2:TE	−1943.71	3925.38	0.00	0.447	—
	2	A + A^2 + LS + TE + C + A:LS + A:TE + A^2:LS	−1945.38	3926.51	1.13	0.254	1.76
	3	A + A^2 + LS + TE + A:LS + A:TE + A^2:LS + A^2:TE	−1952.68	3928.10	2.72	0.115	3.89
	4	A + A^2 + LS + TE + A:LS + A:TE + A^2:LS	−1953.82	3928.25	2.87	0.106	4.22
b) Lyre length	1	A + A^2 + LS + TE + A:LS + A:TE + A^2:LS	−1318.24	2657.11	0.00	0.289	—
	2	A + A^2 + LS + TE + A:LS + A:TE + A^2:LS + A^2:TE	−1317.31	2657.38	0.27	0.253	1.14
	3	A + A^2 + LS + TE + A^2:LS + A^2:TE	−1319.63	2657.77	0.66	0.208	1.39
	4	A + A^2 + LS + TE + A:TE + A^2:LS + A^2:TE	−1318.93	2658.48	1.37	0.146	1.98
	5	A + A^2 + LS + TE + A:LS + A^2:LS + A^2:TE	−1319.62	2659.87	2.76	0.073	3.96
c) Blue chroma	1	A + A^2 + LS + C + A:LS	−794.86	1618.93	0.00	0.193	—
	2	A + A^2 + TE + C	−796.86	1620.78	1.84	0.077	2.51
	3	A + A^2 + LS + C + A:LS + A^2:LS	−794.82	1621.05	2.11	0.067	2.88
	4	A + LS + C + A:LS	−797.01	1621.07	2.14	0.066	2.92
	5	A + A^2 + LS + TE + C + A:LS	−794.85	1621.11	2.17	0.065	2.97
	6	A + LS + TE + C + A:LS + A:TE	−794.86	1621.13	2.19	0.064	3.02
	7	A + A^2 + TE + C + A:TE	−796.32	1621.86	2.92	0.045	4.29
	8	A^2 + TE + C	−798.66	1622.23	3.29	0.037	5.22
	9	A + LS + TE + C + A:TE	−796.64	1622.51	3.57	0.032	6.03
	10	A + A2 + LS + C	−797.86	1622.77	3.83	0.028	6.89
	11	A + A^2 + TE + C + A^2:TE	−796.84	1622.91	3.97	0.026	7.42
	12	A + A^2 + TE + C + A:LS	−796.85	1622.92	3.99	0.026	7.42
	13	A + A^2 + LS + TE + C + A:LS + A:TE	−794.69	1622.97	4.03	0.026	7.42
	14	A + A^2 + LS + TE	−797.97	1623.00	4.07	0.025	7.72
	15	A + A^2 + C	−799.13	1623.17	4.23	0.023	8.39
	16	A + A^2 + LS + TE + C + A:LS + A^2:TE	−794.82	1623.22	4.29	0.023	8.39
	17	A + A^2 + LS + TE + C + A:LS + A^2:LS	−794.82	1623.23	4.30	0.022	8.77
	18	A + A^2 + TE + C + A:TE + A^2:TE	−796.04	1623.48	4.55	0.020	9.65
	19	A + A^2 + LS + TE + C + A:TE	−796.23	1623.85	4.92	0.016	12.06
	20	A^2 + TE + C + A^2:TE	−798.66	1624.38	5.45	0.013	14.85
	21	A^2 + LS + TE + C + A^2:LS	−797.66	1624.53	5.60	0.012	16.08
	22	A + A^2 + LS + C + A^2:LS	−797.71	1624.65	5.71	0.011	17.55
	23	A + A^2 + LS + TE + C + A^2:LS	−796.75	1624.91	5.97	0.010	19.30
	24	A + A^2 + LS + TE + C + A^2:TE	−796.84	1625.07	6.14	0.009	21.44
	25	A^2 + LS + TE + C + A^2:TE	−797.95	1625.13	6.19	0.009	21.44
	26	A + A^2 + LS + TE + C + A:LS + A:TE + A^2:LS	−794.68	1625.15	6.22	0.009	21.44
	27	A + A^2 + LS + TE + C + A:LS + A:TE + A^2:TE	−794.68	1625.16	6.23	0.009	21.44
	28	A + A^2 + LS + TE + C + A:LS + A^2:LS + A^2:TE	−794.78	1625.36	6.43	0.008	24.13
	29	A + A^2 + LS + TE + C + A:TE + A^2:TE	−795.95	1625.49	6.56	0.007	27.57
	30	A + A^2 + LS + TE + C + A:TE + A^2:LS	−796.09	1625.76	6.83	0.006	32.17
d) Eye comb size	1	A + A^2 + LS + A^2:LS	−515.36	1045.04	0.00	0.234	—

	2	$A + A^2$	−518.00	1046.17	1.13	0.132	1.77
	3	$A + A^2 + LS + TE + A^2{:}LS$	−515.36	1047.13	2.09	0.082	2.85
	4	$A + A^2 + LS + A{:}LS + A^2{:}LS$	−515.36	1047.13	2.09	0.082	2.85
	5	$A + A^2 + LS$	−517.59	1047.41	2.37	0.071	3.30
	6	$A + A^2 + TE$	−517.77	1047.78	2.74	0.059	3.97
	7	$A + A^2 + LS + TE + A{:}TE + A^2{:}LS$	−514.85	1048.22	3.18	0.048	4.88
	8	$A + A^2 + LS + TE + A^2{:}LS + A^2{:}TE$	−515.27	1049.06	4.02	0.031	7.55
	9	$A + A^2 + LS + TE + A{:}LS + A^2{:}LS$	−515.35	1049.22	4.18	0.029	8.07
	10	$A + A^2 + LS + A{:}LS$	−517.54	1049.40	4.36	0.026	9.00
	11	$A + A^2 + LS + TE + A{:}LS + A{:}TE + A^2{:}LS$	−514.39	1049.41	4.36	0.026	9.00
	12	$A + A^2 + LS + TE$	−517.58	1049.48	4.44	0.025	9.36
	13	$A + A^2 + TE + A{:}TE$	−517.62	1049.55	4.51	0.024	9.75
	14	$A + A^2 + TE + A^2{:}TE$	−517.65	1049.62	4.58	0.024	9.75
	15	$A + A^2 + LS + TE + A{:}TE + A^2{:}LS + A^2{:}TE$	−514.85	1050.33	5.29	0.017	13.76
	16	$A + A^2 + LS + TE + A{:}TE$	−517.26	1050.93	5.89	0.012	19.50
	17	$A + A^2 + LS + TE + A{:}LS + A{:}TE + A^2{:}LS + A^2{:}TE$	−514.13	1051.02	5.98	0.012	19.50
	18	$A + A^2 + LS + TE + A{:}LS + A^2{:}LS + A^2{:}TE$	−515.27	1051.17	6.13	0.011	21.27
	19	$A + A^2 + LS + TE + A^2{:}TE$	−517.42	1051.25	6.21	0.010	23.40
	20	$A + A^2 + LS + TE + A{:}LS$	−517.53	1051.48	6.44	0.009	26.00
	21	$A + A^2 + TE + A{:}TE + A^2{:}TE$	−517.58	1051.58	6.54	0.009	26.00
e) Tarsus length	1	TE	−609.62	1227.34	0.00	0.147	—
	2	LS + TE	−609.23	1228.63	1.29	0.077	1.91
	3	TE + C	−603.06	1228.85	1.51	0.069	2.13
	4	A + TE	−609.43	1229.03	1.69	0.063	2.33
	5	A^2 + TE	−609.61	1229.39	2.05	0.053	2.77
	6	A	−610.81	1229.73	2.39	0.044	3.34
	7	A^2 + LS + TE	−609.18	1230.59	3.25	0.029	5.07
	8	LS + TE + C	−602.90	1230.67	3.32	0.028	5.25
	9	A + LS + TE	−609.23	1230.69	3.35	0.028	5.25
	10	A + TE + C	−602.99	1230.85	3.51	0.025	5.88
	11	$A + A^2$ + TE	−609.36	1230.95	3.61	0.024	6.13
	12	A^2 + TE + C	−603.05	1230.98	3.64	0.024	6.13
	13	A + TE + A:TE	−609.40	1231.02	3.68	0.023	6.39
	14	null	−612.53	1231.13	3.79	0.022	6.68
f) Lek attendance	1	$A + A^2 + LS + TE + A{:}LS + A^2{:}LS + A^2{:}TE$	−3632.76	7283.98	0.00	0.529	—
	2	$A + A^2 + LS + TE + A{:}LS + A{:}TE + A^2{:}LS$	−3633.54	7285.54	1.56	0.242	2.19
	3	$A + A^2 + LS + TE + A{:}LS + A{:}TE + A^2{:}LS + A^2{:}TE$	−3632.57	7285.70	1.72	0.223	2.37
g) Fighting rate	1	$A + A^2 + LS + TE + A{:}LS + A^2{:}TE$	−1208.18	2432.84	0.00	0.387	—
	2	$A + A^2 + LS + TE + A{:}LS + A{:}TE + A^2{:}TE$	−1207.74	2434.09	1.25	0.208	1.86
	3	$A + A^2 + LS + TE + A{:}LS + A^2{:}LS + A^2{:}TE$	−1208.10	2434.80	1.95	0.146	2.65
	4	$A + A^2 + LS + TE + A{:}LS + A{:}TE + A^2{:}LS + A^2{:}TE$	−1207.71	2436.17	3.33	0.073	5.30
	5	$A + A^2 + TE + A^2{:}TE$	−1212.04	2436.36	3.52	0.067	5.78
	6	$A + A^2 + TE + A{:}TE + A^2{:}TE$	−1211.77	2437.91	5.07	0.031	12.48
	7	$A + A^2 + LS + TE + A^2{:}TE$	−1212.04	2438.46	5.61	0.023	16.83
	8	$A + A^2 + LS + TE + A{:}TE + A^2{:}TE$	−1211.65	2439.78	6.94	0.012	32.25
h) Distance*	1	$A + A^2$	−499.10	1008.39	0.00	0.190	—
	2	A + LS + A:LS	−498.64	1009.56	1.17	0.106	1.79
	3	A + LS + TE + A:LS	−497.72	1009.81	1.41	0.094	2.02

	4	$A + A^2 + TE$	−499.07	1010.43	2.03	0.069	2.75
	5	$A + A^2 + LS$	−499.10	1010.47	2.08	0.067	2.84
	6	A	−501.24	1010.60	2.21	0.063	3.02
	7	$A + A^2 + LS + A:LS$	−498.50	1011.37	2.98	0.043	4.42
	8	$A + LS + TE + A:LS + A:TE$	−497.69	1011.87	3.48	0.033	5.76
	9	$A + A^2 + LS + TE + A:LS$	−497.70	1011.89	3.49	0.033	5.76
	10	$A + A^2 + TE + A:TE$	−498.94	1012.25	3.85	0.028	6.79
	11	$A + A^2 + TE + A^2:TE$	−499.00	1012.38	3.99	0.026	7.31
	12	$A + A^2 + LS + TE$	−499.02	1012.42	4.03	0.025	7.60
	13	$A + TE$	−501.13	1012.47	4.07	0.025	7.60
	14	$A + A^2 + LS + A^2:LS$	−499.09	1012.55	4.16	0.024	7.92
	15	$A + LS$	−501.22	1012.64	4.25	0.023	8.26
	16	$A + A^2 + LS + A:LS + A^2:LS$	−498.50	1013.48	5.09	0.015	12.67
	17	$A + A^2 + LS + TE + A:LS + A:TE$	−497.51	1013.64	5.24	0.014	13.57
	18	$A + A^2 + TE + A:TE + A^2:TE$	−498.66	1013.80	5.40	0.013	14.62
	19	$A + A^2 + LS + TE + A:LS + A^2:TE$	−497.63	1013.87	5.47	0.012	15.83
	20	$A + A^2 + LS + TE + A:TE$	−498.74	1013.97	5.57	0.012	15.83
	21	$A + A^2 + LS + TE + A:LS + A^2:LS$	−497.69	1013.98	5.59	0.012	15.83
	22	$A + TE + A:TE$	−500.95	1014.18	5.78	0.011	17.27
	23	$A + A^2 + LS + TE + A^2:TE$	−498.97	1014.43	6.04	0.009	21.11
	24	$A + LS + TE$	−501.10	1014.48	6.09	0.009	21.11
	25	$A + A^2 + LS + TE + A^2:LS$	−499.02	1014.52	6.12	0.009	21.11

Note: A = age, LS = lifespan, TE = terminal event, C = cohort. Interactions are denoted by colons. Individual identity nested in study site was fitted as a random effect in all models.

* Territory distance from the lek center (sqrt transformed).

Online Table A3. A suite of best candidate models ($\Delta AIC_c \leq 7$) predicting the relative change in morphological (a–d) and behavioural (e–g) traits between subsequent years with the log-likelihood estimate, AIC_c values, ΔAIC_c, model weights and evidence ratios (ER). Tarsus length was not included in the rate of change analysis, as the first analysis did not indicate significant age-dependence.

Analysis	Rank	Model	LogLik	AIC_c	ΔAIC_c	Weight	ER
a) Body mass	1	$A + A^2 + Cohort$	322.11	−618.43	0.00	0.086	–
	2	$A + A^2 + TE + A^2:TE + Cohort$	324.13	−617.84	0.59	0.064	1.34
	3	$A + A^2 + TE + Cohort$	322.94	−617.79	0.64	0.063	1.37
	4	$A + A^2 + LS + TE$	315.92	−617.22	1.21	0.047	1.82
	5	$A + A^2 + LS + TE + Cohort$	323.72	−617.01	1.42	0.043	2.00
	...						
	59	$A + LS + TE + A:LS + Cohort$	321.07	−611.72	6.71	0.003	28.67
b) Lyre length	1	$A + A^2 + LS + TE + A^2:LS + A^2:TE$	263.60	−508.15	0.00	0.264	–
	2	$A + A^2 + LS + A:LS + A^2:LS$	261.85	−506.87	1.28	0.139	1.90

	3	A + A^2 + LS + A:LS	260.56	−506.48	1.66	0.115	2.30
	4	A + A^2 + LS + TE + A:TE + A^2:LS + A^2:TE	263.74	−506.20	1.94	0.100	2.64
	5	A + A^2 + LS + TE + A:LS + A^2:LS + A^2:TE	263.62	−505.95	2.19	0.088	3.00
	...						
	14	A + A^2 + TE + A^2:TE	258.01	−501.37	6.77	0.009	29.33
c) Blue chroma	1	A + LS	127.31	−244.27	0.00	0.112	—
	2	LS	126.23	−244.23	0.03	0.110	1.02
	3	A	126.19	−244.15	0.12	0.105	1.07
	4	A + TE	126.99	−243.63	0.64	0.081	1.38
	5	LS + TE	126.83	−243.32	0.95	0.070	1.60
	...						
	23	A^2 + LS + TE + A^2:TE	126.93	−239.21	5.06	0.009	12.44
	24	null	122.51	−238.90	5.39	0.008	14.00
d) Eye comb size	1	A + A^2 + Cohort	−266.21	558.26	0.00	0.221	—
	2	A + A^2 + LS + Cohort	−266.11	560.39	2.13	0.076	2.91
	3	A + A^2 + TE + Cohort	−266.16	560.48	2.22	0.073	3.03
	4	A + A^2 + TE + A^2:TE + Cohort	−264.98	560.48	2.23	0.073	3.03
	5	A + Cohort	−268.79	561.14	2.88	0.053	4.17
	...						
	30	A + A^2 + LS + TE + A:TE + A:LS + A^2:TE + Cohort	−263.69	565.11	6.85	0.007	31.57
e) Lek attendance	1	A	−97.07	202.42	0.00	0.095	—
	2	A + A^2	−96.05	202.52	0.11	0.090	1.06
	3	A + LS + A:LS	−95.07	202.74	0.33	0.081	1.17
	4	A + LS + TE + A:LS	−93.98	202.77	0.35	0.080	1.19
	5	A + TE	−96.29	203.00	0.58	0.071	1.34
	...						
	35	A + A^2 + LS + TE + A:TE + A^2:LS + A^2:TE	−93.62	208.86	6.45	0.004	23.75
f) Fighting rate	1	A^2 + Cohort	47.00	−72.23	0.00	0.122	—
	2	Cohort	45.29	−71.15	1.09	0.071	1.72
	3	A + A^2 + Cohort	47.61	−71.09	1.14	0.069	1.77
	4	A^2 + TE + Cohort	47.23	−70.34	1.89	0.047	2.60
	5	A + A^2	40.24	−70.03	2.21	0.041	2.98
	6	A^2 + LS + Cohort	47.01	−69.89	2.34	0.038	3.21
	7	null	38.03	−69.88	2.35	0.038	3.21
g) Distance	1	A + TE	−143.94	298.35	0.00	0.068	—
	2	A	−145.05	298.40	0.05	0.066	1.03
	3	A^2 + LS + TE + A^2:LS	−141.82	298.52	0.17	0.062	1.10
	4	A^2 + LS + A^2:LS	−143.09	298.85	0.49	0.053	1.28
	5	A + A^2 + LS + TE + A^2:LS	−141.19	299.53	1.17	0.038	1.79
	...						
	15	A + A^2 + LS + TE + A:LS + A:TE + A^2:TE	−139.38	300.53	2.18	0.023	2.96
	16	null	−147.22	300.61	2.26	0.022	3.09

Online Table A4. The relative importance, coefficient estimates, standard errors (SE) and effect sizes (Pearson's r with 95% CI) of the fixed effects of age, lifespan (LS), terminal event (TE), cohort and the relevant interactions (denoted by colons) on the rate of change

808 of morphological (a–d) and behavioral traits (e–g) after model averaging. Statistically
809 significant effects (95 % CI does not overlap with 0) are in bold. Tarsus length was not
810 included in the rate of change analysis, as the first analysis did not indicate significant age-
811 dependence.

Model	Parameter	Relative importance	Estimate	SE	Effect size, r (95% CI)
a) Body mass, n = 108	Intercept	—	0.09	0.13	—
id:site var = 0.000	**Age**	**1.00**	**−0.78**	**0.33**	**0.25 (−0.44, −0.04)**
residual var = 0.002	Age^2	0.96	0.94	0.58	0.18 (−0.04, 0.37)
	LS	0.63	0.17	0.31	0.06 (−0.16, 0.27)
	TE	0.74	0.23	0.18	0.14 (−0.07, 0.34)
	Age:LS	0.24	−0.52	0.80	−0.07 (−0.28, 0.15)
	Age:TE	0.22	−0.89	0.89	−0.11 (−0.31, 0.11)
	Age^2:LS	0.22	−0.10	0.39	−0.03 (−0.24, 0.19)
	Age^2:TE	0.30	−0.79	0.63	−0.14 (−0.34, 0.08)
	Cohort	0.62	—	—	—
b) Lyre length, n = 106	Intercept	—	−0.04	0.19	—
id:site var = 0.000	**Age**	**1.00**	**−1.60**	**0.45**	**−0.38 (−0.54, −0.17)**
residual var = 0.003	**Age^2**	**1.00**	**4.22**	**1.05**	**0.42 (0.22, 0.57)**
	LS	0.96	0.55	0.37	0.17 (−0.06, 0.37)
	TE	0.70	0.38	0.28	0.15 (−0.07, 0.36)
	Age:LS	0.34	−0.56	1.00	−0.06 (−0.28, 0.16)
	Age:TE	0.20	0.24	0.44	0.06 (−0.16, 0.28)
	Age^2:LS	**0.95**	**−3.37**	**1.17**	**−0.31 (−0.49, −0.10)**
	Age^2:TE	**0.52**	**−1.76**	**0.84**	**−0.23 (−0.42, −0.01)**
c) Blue chroma, n = 106	Intercept	—	0.20	0.18	—
id:site var = 0.000	**Age**	**0.69**	**−0.55**	**0.34**	**−0.19 (−0.39, −0.04)**
residual var = 0.014	Age^2	0.31	0.23	0.76	0.04 (−0.19, 0.26)
	LS	0.65	−0.43	0.35	−0.14 (−0.35, 0.09)
	TE	0.41	0.02	0.31	0.01 (−0.22, 0.23)
	Age:LS	0.09	0.50	0.76	0.08 (−0.15, 0.29)
	Age:TE	0.08	−0.41	0.51	−0.09 (−0.31, 0.14)
	Age^2:LS	0.05	−0.93	1.89	−0.06 (−0.28, 0.17)
	Age^2:TE	0.02	0.65	1.56	0.05 (−0.18, 0.27)
d) Eye comb size, n = 105	Intercept	—	−4.51	3.32	—
id:site var = 0.000	**Age**	**1.00**	**−15.17**	**5.68**	**−0.29 (−0.47, −0.08)**
residual var = 1.055	Age^2	0.85	16.45	11.50	0.16 (−0.06, 0.36)
	LS	0.49	3.62	6.10	0.07 (−0.15, 0.28)
	TE	0.54	6.82	4.18	0.10 (−0.12, 0.31)
	Age:LS	0.16	−6.63	18.09	−0.04 (−0.26, 0.18)
	Age:TE	0.14	−4.40	8.60	−0.06 (−0.27, 0.16)
	Age^2:LS	0.13	−16.87	20.62	−0.09 (−0.30, 0.13)
	Age^2:TE	0.24	−22.73	14.63	−0.17 (−0.37, 0.05)
	Cohort	1.00	—	—	—
e) Lek attendance, n = 86	Intercept	—	0.41	0.98	—
id:site var = 0.000	Age	0.99	−4.96	2.64	−0.23 (−0.44, 0.02)
residual var = 0.205	Age^2	0.50	1.65	4.57	0.05 (−0.20, 0.28)
	LS	0.57	1.89	2.40	0.10 (−0.15, 0.33)
	TE	0.60	1.34	1.34	0.13 (−0.12, 0.35)

	Age:LS	0.32	5.85	3.96	0.18 (−0.07, 0.40)
	Age:TE	0.23	−2.62	2.66	−0.12 (−0.35, 0.13)
	Age^2:LS	0.07	−1.08	9.33	−0.01 (−0.26, 0.23)
	Age^2:TE	0.10	4.82	6.26	0.10 (−0.15, 0.33)
f) Fighting rate, n = 76	Intercept	—	13.40	10.35	—
id:site var = 0.000	Age	0.57	−8.57	4.73	−0.25 (−0.47, 0.03)
residual var = 0.029	Age^2	0.74	15.87	8.77	0.25 (−0.03, 0.47)
	LS	0.20	−4.38	6.69	−0.09 (−0.35, 0.18)
	TE	0.58	−5.52	3.87	−0.20 (−0.43, 0.08)
	Age:TE	0.11	12.66	9.02	0.19 (−0.08, 0.43)
	Cohort	0.53	—	—	—
g) Distance*, n = 81	Intercept	—	1.34	1.90	—
id:site var = 0.000	Age	0.68	5.86	5.97	0.13 (−0.13, 0.37)
residual var = 0.425	Age^2	0.55	−4.47	12.91	−0.05 (−0.30, 0.21)
	LS	0.63	−4.41	4.94	−0.12 (−0.36, 0.14)
	TE	0.64	−3.53	2.65	−0.18 (−0.41, 0.09)
	Age:LS	0.14	−19.25	11.56	−0.22 (−0.44, 0.04)
	Age:TE	0.09	−2.70	7.66	−0.05 (−0.30, 0.21)
	Age^2:LS	**0.32**	**26.20**	**11.36**	**0.30 (0.04, 0.50)**
	Age^2:TE	0.14	12.72	10.14	0.17 (−0.10, 0.40)

Notes: All parameter values were rescaled by multiplying the original values by 10 to obtain more informative coefficient estimates and standard errors. Random effects are presented as id:site and residual variances in the final model. * Territory distance from the lek center.

Online Table A5. A suite of best candidate models ($\Delta AIC_c \leq 7$) testing for potential senescence in morphological (a–d) and behavioural (e–g) traits with the log-likelihood estimate, AIC_c values, ΔAIC_c, model weights and evidence ratios (ER). For lek attendance, one candidate model had a superior model fit and multimodel inference was not required. Tarsus length was not included in the rate of change analysis, as the first analysis did not indicate significant age-dependence.

Analysis	Rank	Model	LogLik	AIC_c	ΔAIC_c	Weight	ER
a) Body mass	1	Age + TE + Age:TE	−552.32	1117.46	0.00	0.396	—
	2	Age + LS + TE + Age:TE	−551.73	1118.56	1.10	0.228	1.74
	3	Age + LS + TE + Age:LS + Age:TE	−550.71	1118.84	1.38	0.199	1.99
	4	Age + TE	−555.20	1120.99	3.52	0.068	5.82
	5	Age + LS + TE	−554.23	1121.27	3.80	0.059	6.71
	6	Age + LS + TE + Age:LS	−553.38	1121.86	4.40	0.044	9.00
b) Lyre length	1	Age	−408.88	826.11	0.00	0.247	—
	2	Age + LS	−408.03	826.58	0.48	0.195	1.27
	3	Age + TE + Age:TE	−407.36	827.47	1.36	0.125	1.98
	4	Age + LS + TE + Age:TE	−406.30	827.62	1.51	0.116	2.13
	5	Age + TE	−408.82	828.17	2.06	0.088	2.81
	6	Age + LS + Age:LS	−407.98	828.72	2.61	0.067	3.69
	7	Age + LS + TE	−408.02	828.79	2.69	0.064	3.86

	8	Age + LS + TE + Age:LS + Age:TE	−406.11	829.53	3.43	0.044	5.61
	9	Age + LS + TE + Age:LS	−407.96	830.94	4.83	0.022	11.23
	10	LS + TE	−410.36	831.26	5.15	0.019	13.00
c) Blue chroma	1	Age + LS + Cohort	−314.27	652.42	0.00	0.336	—
	2	Age + LS + TE + Cohort	−313.90	654.05	1.63	0.149	2.26
	3	Age + LS + TE + Cohort + Age:TE	−312.81	654.26	1.83	0.134	2.51
	4	Age + Cohort	−316.52	654.59	2.17	0.113	2.97
	5	Age + LS + Cohort + Age:LS	−314.23	654.70	2.27	0.108	3.11
	6	Age + LS + TE + Cohort + Age:LS	−313.80	656.24	3.81	0.050	6.72
	7	Age + LS + TE + Cohort + Age:LS + Age:TE	−312.77	656.60	4.17	0.042	8.00
	8	Age + TE + Cohort	−316.51	656.90	4.47	0.036	9.33
	9	Age + TE + Cohort + Age:TE	−315.46	657.16	4.74	0.031	10.84
d) Eye comb size	1	Age	−163.29	334.97	0.00	0.307	—
	2	Age + TE + Age:TE	−161.47	335.80	0.82	0.203	1.51
	3	Age + TE	−162.76	336.12	1.15	0.173	1.77
	4	Age + LS	−163.29	337.18	2.20	0.102	3.01
	5	Age + LS + TE + Age:TE	−161.46	338.06	3.09	0.065	4.72
	6	Age + LS + TE	−162.73	338.30	3.33	0.058	5.29
	7	Age + LS + Age:LS	−163.16	339.18	4.20	0.037	8.30
	8	Age + LS + TE + Age:LS + Age:TE	−161.18	339.84	4.87	0.027	11.37
	9	Age + LS + TE + Age:LS	−162.46	340.05	5.08	0.024	12.79
e) Lek attendance	1	Age + LS + TE + Age:LS + Age:TE	−813.74	1642.40	0.00	0.986	—
f) Fighting rate	1	Age + LS + TE + Age:LS + Age:TE	−475.14	965.11	0.00	0.681	—
	2	Age + LS + TE + Age:TE	−477.55	967.71	2.60	0.186	3.66
	3	Age + TE + Age:TE	−479.01	968.46	3.34	0.128	5.32
g) Distance*	1	Age + TE + Age:TE	−176.92	366.55	0.00	0.618	—
	2	Age + LS + TE + Age:TE	−176.66	368.29	1.73	0.260	2.38
	3	Age + LS + TE + Age:LS + Age:TE	−176.57	370.40	3.84	0.090	6.87

Note: LS = lifespan, TE = terminal event. Interactions are denoted by colons. Individual identity nested in study site was fitted as a random effect in all models. * Territory distance from the lek center (sqrt transformed).

Online Table A6. The relative importance, coefficient estimates, standard errors (SE) and effect sizes (Pearson's r with 95 % CI) of the fixed effects of age, lifespan (LS), terminal event (TE), cohort and the relevant interactions (denoted by colons) on morphological (a–d) and behavioral traits (e–g) after model averaging. Model averaging was no required for lek attendance (see Online Table A5 e). Tarsus length was not included in the senescence analysis, as the first analysis did not indicate significant age-dependence.

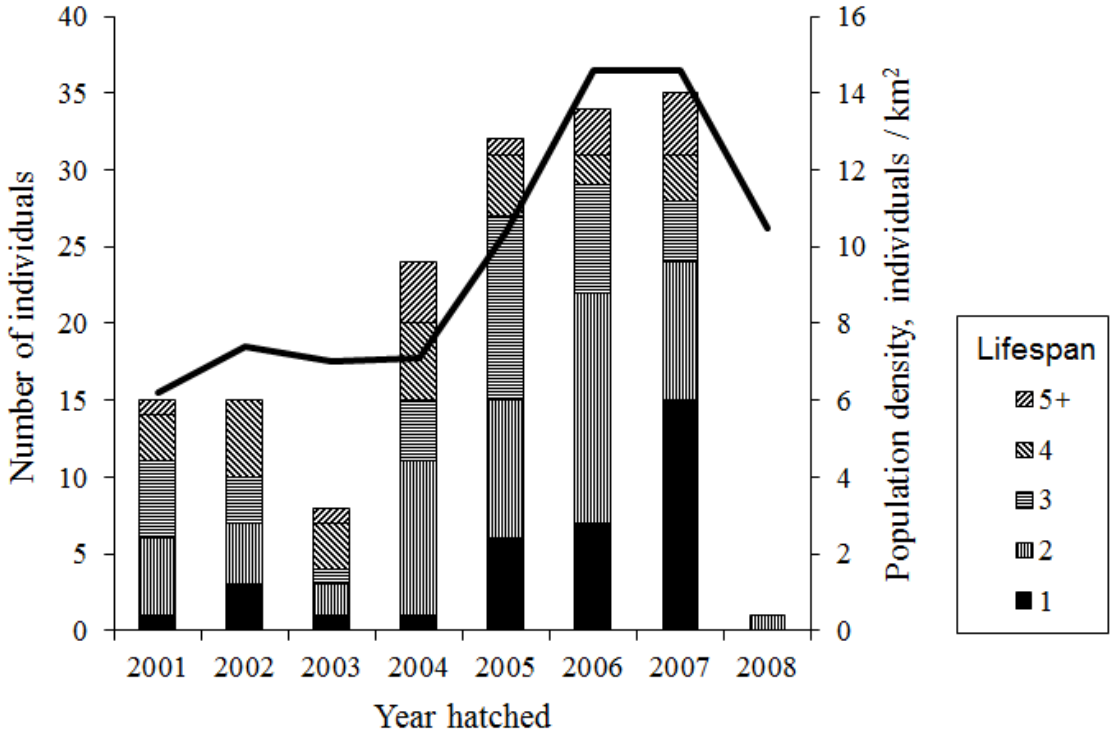
Model	Parameter	Relative importance	Estimate	SE	Effect size, r (95% CI)
a) Body mass, n = 74	Intercept	—	1266.88	6.23	—
54 % survival	**Age**	**1.00**	**−58.20**	**12.14**	**−0.36 (−0.48, −0.21)**
id:site var = 1321.6	LS	0.53	13.99	11.10	0.10 (−0.06, 0.25)
residual var = 402.9	**TE**	**1.00**	**27.91**	**8.34**	**0.26 (0.10, 0.39)**
	Age:LS	0.24	15.86	11.17	0.11 (−0.05, 0.26)
	Age:TE	**0.83**	**34.85**	**13.98**	**0.20 (0.04, 0.34)**

b) Lyre length, n = 73	Intercept	—	224.32	1.10	—
60 % survival	**Age**	**0.98**	**−3.77**	**1.45**	**−0.18 (−0.31, −0.04)**
id:site var = 59.49	LS	0.53	−2.98	2.17	−0.10 (−0.23, 0.02)
residual var = 17.71	TE	0.49	−0.28	1.60	−0.01 (−0.15, 0.13)
	Age:LS	0.14	−0.97	2.39	−0.03 (−0.16, 0.11)
	Age:TE	0.29	4.14	2.23	0.13 (−0.01, 0.26)
c) Blue chroma, n = 76	Intercept	—	26.49	0.58	—
72 % survival	**Age**	**1.00**	**−2.07**	**0.37**	**−0.48 (−0.61, −0.32)**
id:site var = 0.91	**LS**	**0.82**	**−0.89**	**0.39**	**−0.22 (−0.39, −0.02)**
residual var = 2.83	TE	0.44	−0.31	0.39	−0.08 (−0.27, 0.12)
	Age:LS	0.20	−0.21	0.63	−0.15 (−0.33, 0.05)
	Age:TE	0.21	0.96	0.63	0.03 (−0.16, 0.22)
	Cohort	1.00	—	—	—
d) Eye comb size, n = 73	Intercept	—	4.39	0.16	—
47 % survival	**Age**	**1.00**	**−0.88**	**0.27**	**−0.31 (−0.46, −0.12)**
id:site var = 1.01	LS	0.31	0.20	0.23	0.09 (−0.11, 0.27)
residual var = 0.48	TE	0.55	0.61	0.36	0.16 (−0.03, 0.34)
	Age:LS	0.09	0.04	0.29	0.01 (−0.18, 0.20)
	Age:TE	0.30	0.23	0.37	0.06 (−0.13, 0.25)
e) Lek attendance, n = 76	Intercept	—	3.75	0.84	—
61 % survival	**Age**	**1.00**	**−4.81**	**0.45**	**−0.61 (−0.69, −0.50)**
id:site var = 2.42	LS	1.00	−0.10	0.22	−0.03 (−0.17, 0.11)
residual var = 1.00	**TE**	**1.00**	**−0.74**	**0.25**	**−0.21 (−0.33, −0.06)**
	Age:LS	**1.00**	**0.92**	**0.10**	**0.57 (0.46, 0.66)**
	Age:TE	**1.00**	**0.74**	**0.13**	**0.39 (0.25, 0.50)**
f) Fighting rate, n = 76	Intercept	—	−1.12	0.10	—
72 % survival	**Age**	**1.00**	**−0.80**	**0.16**	**−0.46 (−0.60, −0.29)**
id:site var = 0.36	**LS**	**0.87**	**0.38**	**0.18**	**0.21 (0.01, 0.39)**
residual var = 1.00	TE	1.00	0.11	0.11	0.11 (−0.10, 0.30)
	Age:LS	**0.68**	**0.36**	**0.16**	**0.22 (0.02, 0.40)**
	Age:TE	**1.00**	**0.65**	**0.15**	**0.41 (0.22, 0.55)**
g) Distance*, n = 76	Intercept	—	3.76	0.17	—
59 % survival	**Age**	**1.00**	**1.26**	**0.20**	**0.36 (0.24, 0.46)**
id:site var = 1.30	LS	0.36	−0.24	0.32	−0.04 (−0.16, 0.07)
residual var = 0.29	TE	1.00	−0.00	0.19	−0.00 (−0.12, 0.12)
	Age:LS	0.09	−0.13	0.30	−0.03 (−0.14, 0.09)
	Age:TE	**1.00**	**−0.99**	**0.27**	**−0.21 (−0.32, −0.09)**

Note: Individual identity nested in study site was fitted as a random effect in all models. Parameter values of blue chroma were rescaled by multiplying the original values by 100 to obtain more informative coefficient estimates and standard errors. Random effects are represented as id:site and residual variances in the full model. Survival percentage indicates what proportion of males survived until the year after the peak trait expression. * Territory distance from the lek center (sqrt transformed).

Online Figure A1. Number of individuals with different lifespans in our sample by the year of hatching (bars, see label). Lifespans of 5 and 6 years have been pooled into class 5. The line represents the local population density in August of the hatching year.

841 Recruitment in 2008 was very low due to harsh weather conditions after hatching, which is
842 reflected in the decreased population density and the very small sample size in our data.



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